VEGETATION AND FLORA OF THE SONORAN DESERT

FORREST SHREVE AND IRA L. WIGGINS

VOLUME I

VEGETATION OF THE SONORAN DESERT

Forrest Shreve

CARNEGIE INSTITUTION OF WASHINGTON PUBLICATION 591
WASHINGTON, D. C.
1951

VEGETATION AND FLORA OF THE SONORAN DESERT

FORREST SHREVE AND IRA L. WIGGINS

VOLUME I

VEGETATION OF THE SONORAN DESERT

Forrest Shreve

CARNEGIE INSTITUTION OF WASHINGTON PUBLICATION 591
WASHINGTON, D. C.
1951

THE WILLIAM BYRD PRESS, INC., RICHMOND, VIRGINIA
THE STANDARD ENGRAVING COMPANY, WASHINGTON, D. C.

VOLUME I

VEGETATION OF THE SONORAN DESERT

Foreword

Forrest Shreve dedicated virtually his entire scientific career to the study of the botanical features of the arid regions of North America. In this pursuit he exhibited a unique allegiance and fealty to his subject and developed a broad plan of investigation which grew with the years both in intensity and in breadth of vision. During almost forty years he devoted a large portion of his effort to extensive field investigations, carried out under very primitive and rugged conditions. As his knowledge of the southwestern deserts grew, Shreve became more and more convinced of the necessity of living in the region during all seasons in order to gain a full appreciation of the biocoenose of these areas. In reply to a suggestion that it might be more comfortable for him to live in California and visit the deserts on occasional expeditions, he wrote: "I now have at Tucson living material of scores of the outlying parts of our area, from which I am learning much in regard to life histories, ecological habits, and physiological behavior which would remain unknown if they had merely been observed and collected on a field expedition. It is essential that this work be carried on under natural desert conditions. I feel very strongly that it is only by thus learning our plants as intimately as possible that we can hope to make our study of vegetation of the Sonoran Region contribute a fresh and vital view of the play of evolutionary processes under arid conditions." Shreve thus became thoroughly inured to life in the desert, although this was far removed from his native haunts and early environment.

Dr. Shreve was born in Easton, on the eastern shore of Maryland, July 8, 1878. He attended the Johns Hopkins University and was graduated A.B. in 1901. From the same institution he received the Ph.D. in 1905. While holding the Adam T. Bruce Fellowship of the Johns Hopkins University and during two later periods he worked in the Blue Mountain Region at Cinchona, Jamaica, the Tropical Station of the New York Botanical Garden. The results of these investigations were published in *A Montane Rain-Forest* (Carnegie Institution of Washington Publication 199, 1914). Shreve always maintained his interest in the Hopkins, and later collaborated with Professors D. S. Johnson and Burton E. Livingston. Jointly with the latter he published *The Distribution of Vegetation in the United States, As Related to Climatic Conditions* (Carnegie Institution of Washington Publication 284, 1921).

Dr. Shreve served as associate professor of botany in Goucher College 1906 to 1908, and joined the staff of the Desert Laboratory of the Carnegie Institution of Washington, at Tucson, Arizona, in 1909. He retained his connection with the Institution until his retirement in 1945, and continued his work in his chosen field until his death, July 19, 1950. He was editor of *The Plant World* 1911 to 1919, and was president of the Ecological Society in 1921.

It is evident from Shreve's publications on various aspects of the botanical

features of the southwestern deserts that his vision of the basic scientific concepts involved underwent profound development. The role of arid conditions in the evolution of the flora of the region and the migration of plants from the humid areas seemed more and more to attract his interest. These investigations entailed the close co-operation of experts on the floristics of the several regions involved and on ecological and plant geographical studies. Shreve accordingly developed a plan to cover one by one the four North American desert areas, the Sonoran, the Chihuahuan, the Mojave, and the Great Basin Deserts, in order to work out the comparative features of distribution, habitat, and behavior of the plants of the four areas. A comprehensive study of the entire North American Desert from the combined viewpoints of vegetation and flora, and a careful examination of all the evidence that present distribution can give as to historical development of desert plants, were to round out the plan.

In a memorandum outlining this plan of investigation Shreve wrote:

> The project . . . provides for a thorough investigation of the taxonomic and ecological features of the plant life of the most arid part of the North American desert. The aims of the work would be the preparation of a flora of the vascular plants, study and description of the principal plant communities and their distribution, comparative investigation of the habitat requirements of characteristic plants in different parts of the area, and determination of some of the most important environmental conditions related to vegetation. The ultimate objective of the work would be a study of the origin and history of the strongly endemic flora of the region and of the highly specialized structural and physiological features which some of its plants possess.
>
> It is only on the basis of an accurate and reasonably complete taxonomic study of the area that any effort can be made to unravel the sources of origin of its plant life, the paths of migration along which various plant races have entered it, and the extent to which these migrations have been accompanied by evolutionary development. There is evidence that the area concerned has been desert at least since the Miocene, and that it has been the arena of a prolonged combat in which a considerable number of plant families have developed species capable of withstanding arid conditions, while other families have contributed members able to persist in favorable spots or at suitable seasons. There appears to be little hope that the paleontological record will give much aid in reading the history of the origin of the present distinctly desert plants of this region. It is believed that a study of the floristic features, interpreted in terms of the ecological behavior of the plants involved, will do as much as can be done toward unraveling the biological history of the area and its relations to the development of similar plant populations in northern central Mexico and in South America. . . .
>
> It is only through a study of the plant communities and the dominant perennials in relation to the conditions of climate and soil that the processes can be evaluated which have given the plant life of the area its distinctive character.
>
> The Chihuahuan and the Sonoran Deserts constitute parallel paths along which plant races have moved or receded under dissimilar sets of conditions. Their histories have undoubtedly been linked by a common participation in the effects of climatic change. The results of investigation of the two regions would reveal many relationships and contrasts of value in the study of each of the regions, and also be of use in deciphering as much as possible of the history of the entire arid region of North America.

In order to carry this program into effect, Shreve enlisted the co-operation of Professor Ira L. Wiggins, of Stanford University, to cover the floristic work on the Sonoran Desert. The results of Professor Wiggins' studies are to appear in volume II of the present publication. The floristic work in the Chihuahuan Desert was undertaken by Professor Ivan Johnston, of Harvard University. Many of the results of the latter investigation have already been published by Professor Johnston in the *Journal of the Arnold Arboretum.*

Dr. Shreve spent considerable time in the Chihuahuan Desert on investigations of the vegetation of this region, and gathered much information in the course of this work. He also did some work in the Mojave and in the Great Basin. He was, however, unable to complete his studies because conditions imposed by World War II made field work very difficult and finally impossible. Some of his collaborators were also called to other lines of duty during this period. Thereafter, Dr. Shreve's impaired health hindered the resumption of his field studies, and his energies went largely into assembling for publication some of the vast amount of material already in hand. It is most fortunate that under these difficult conditions Dr. Shreve was able to complete this, the first, of his contemplated series of publications comprising his ambitious plan for interpreting some of the biological phenomena of the North American deserts on the basis of ecological and floristic investigation.

January 25, 1951

H. A. Spoehr
Chairman Emeritus, Division of Plant Biology, Carnegie Institution of Washington

Contents

List of Illustrations

Maps

Plates

1

Introduction

INVESTIGATION of the botanical features of the Sonoran Desert was undertaken as a logical step in the development of the work of the Desert Laboratory of the Carnegie Institution of Washington, opened in 1903 and located at Tucson, Arizona. Earlier research at the laboratory was chiefly concerned with the physiological and ecological behavior of some of the characteristic plants of the immediate vicinity and with the conditions to which they are subjected. With the exception of work carried out by MacDougal and collaborators in the Salton Basin and by Shreve in the Santa Catalina Mountains, no extended investigations had been made prior to 1932 outside the grounds of the laboratory and their environs.

The Tucson region is typical of a large part of the Sonoran Desert, and its physical conditions and plant life are more or less closely matched throughout the larger area. A comprehensive study of the flora and vegetation of the Sonoran Desert promised a useful addition to knowledge of arid America. Such an investigation seemed to offer opportunities for greatly increasing information on the relation of climatic and soil conditions to the distribution and activities of desert plants. The work also promised an enumeration of the plant species, a much fuller knowledge of their distributional limits, and a basis for the study of their origin, dispersal, and development.

The enlargement of the field of work has done much to elucidate some of the older problems which confronted investigators at the Desert Laboratory. The plant communities of the Tucson area have been followed into drier situations and to the limits of their distribution. It has been possible to study the influences of different degrees of aridity as well as the margins along which desert plants give way to those of different types. Conversely, it was found that the detailed knowledge which had grown from the thirty years of research at the Desert Laboratory was of great help in studying the poorly known parts of the Sonoran Desert. The background with which the work was approached did much to offset the limitations which are inherent in the expeditionary type of research. Early in the work it was realized that very many of the dominant plants in remote parts of the region are known scientifically as to their taxonomic position and in no other respect. An important phase of the investigation has been the effort to learn as much as possible about the life histories of some of these plants. With seeds, living plants, and dry or preserved material collected in the field, it has been possible to study germination, growth, resistance to drought and frost, seasonal habits of foliation and flowering, and anatomical features of stem and leaf.

The project for investigation of the Sonoran Desert was outlined in 1932 and field work was begun in the spring of 1933. The program provided for co-opera-

tion between the Desert Laboratory of the Carnegie Institution of Washington and the Dudley Herbarium of Stanford University, the former to be concerned with the study of the vegetation, the latter with that of the flora. The work on vegetation was carried out by Forrest Shreve and Thomas Dwight Mallery, and responsibility for the elaboration of the flora was assumed by Ira Loren Wiggins. Map 2 shows the extent of the field work. The volume now in the hands of the reader embodies the results of the vegetational work. Volume II constitutes the results of the floristic work of Dr. Wiggins and of several specialists whom he invited to contribute the text for certain groups of plants.

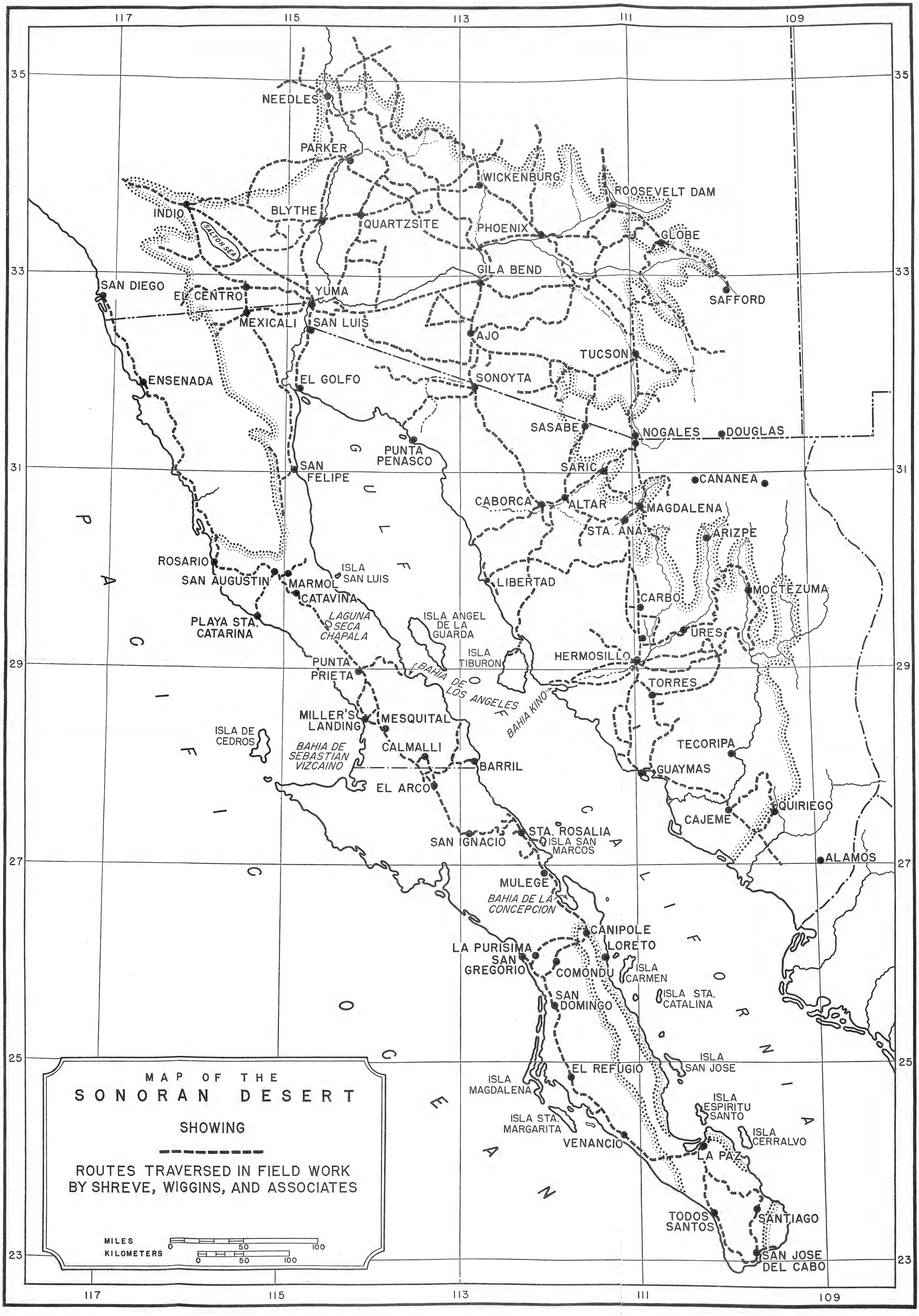
The author wishes to acknowledge the very helpful collaboration given throughout the field work by Fred C. Roberts of Tucson, James W. Manson of Nogales, John Davidson of Guaymas, and Enrique Gayazar of Santa Rosalía.

Boundaries of the Sonoran Desert

The region designated as "Sonoran Desert" was tentatively outlined early in the course of its investigation, and more accurately delimited in later field work. In determining the extent of the region and the location of its boundaries, the only criteria considered were those of its vegetation and flora. The word "desert," which is so commonly used with a definite set of geographic connotations, is here used in a strictly biological sense. The Sonoran Desert is treated as a region of biological unity. The many features of climate, physiography, soils, and hydrography which also distinguish the region from surrounding ones are not a part of its biological character. The word "Sonoran" was used for the area because it has long been employed in physiographic and biological literature in nearly the same sense, because more of the area lies in the Mexican state of Sonora than in any other state, and finally because of its brevity and convenience. There is no relation between the designation "Sonoran Desert" as used in this publication and the "Lower Sonoran Zone" of C. Hart Merriam, although parts of the boundaries of the two are closely coincident.

Harshberger (1911) described the vegetation of North America and published a small-scale map, designating the region here under consideration as "The Sonoran Desert" and giving it approximately the same boundaries that have been adopted in the present publication. Sanders (1921), in discussing the natural regions of Mexico, mapped an area roughly corresponding to the Mexican part of the Sonoran Desert, which he designated as the "Desert of Sonora and Lower California." His desert area extends too far east in Sonora and includes the mountains of Baja California, at the same time that it excludes the coastal fringe of both states. In a study of mammalian distribution and ecology in the southwestern United States, Dice and Blossom (1937) designated as the "Sonoran Province" an area in southern Arizona which corresponds very closely to the Sonoran Desert as delimited in that region. In a publication on the distribution of mammals in Sonora, Burt (1938) outlined, on mammalian evidence, a "Sonoran Biotic Province" which corresponds very closely to the part of the Sonoran Desert that lies in Sonora except that it does not extend so far south in the coastal

MAP 2



Map 2. Routes traversed in field work by Shreve, Wiggins, and associates


12
0

region. Other publications might be cited which would show that the characteristic plant and animal life of the Sonoran Desert and the position of the boundaries of that area have long been recognized by biological workers.

Each section of the boundary of the Sonoran Desert from 75 to 300 km. in length is the limit of some particular type of vegetation and of a group of species. As the boundary is followed farther, it is found to be the limit for other types of vegetation and for different groups of species. There is naturally no single type of vegetation which ranges unchanged over so large an area. Vegetational types often show a close resemblance in physiognomic features at the same time that they differ greatly in floristic composition.

The boundary of the Sonoran Desert is sharply defined wherever the topography is abrupt, as in Arizona between Safford and Wickenburg, in California along the east base of the San Jacinto and Cuyamaca Mountains, in Baja California along the east foot of the Sierra Juárez and Sierra San Pedro Mártir, and in Sonora near the confluence of the Bavispe and Moctezuma Rivers. In level or rolling regions the boundary is ill defined and there is a gradual transition from the desert to adjacent types of vegetation, as in Sonora between Quiriego and the Gulf of California, in Arizona and California in the vicinity of Needles, and in Baja California to the north of Rosario. From the headwaters of the Salt River, in Arizona, southward to Moctezuma, Sonora, the boundary lies at an elevation of 900 to 950 m. All other sections of the boundary lie at lower levels. The well known influence of slope exposure in determining the distribution of vegetation is responsible for many tongues and islands of desert which give irregularity to the boundary in its rugged sections.

In studying vegetation it is more satisfactory to cover a natural area than a political one, since the boundaries of states and provinces are so often straight and independent of natural features of the sort that limit the range of types of vegetation. In the study of the flora, however, there are some inconveniences in adopting a natural area, and taxonomic literature shows that this has not often been done. Hence, in order to enumerate accurately the plants of the Sonoran Desert, it has been necessary to find the precise locality at which a given plant was collected in any one of the four political divisions, and thus to determine whether it was growing inside or outside the desert boundary.

2

Physical Features

Geography

As a geographical entity the Sonoran Desert may be most simply described as the region immediately surrounding the head of the Gulf of California. In the broadest parts the inner boundary is 360 km. (224 mi.) from the Gulf coast in Arizona and 280 km. (175 mi.) from it in Sonora. In Baja California the Desert extends from coast to coast for 540 km. (335 mi.), or approximately the central third of the peninsula. Although a considerable part of the Sonoran Desert faces the Pacific Ocean, the Gulf of California is nevertheless its dominant geographical feature as well as the recipient of a very high percentage of its drainage.

In elevation the Sonoran Desert lies below 915 m. (3000 ft.) except for the narrow band along the eastern edge in Arizona and in northern Sonora, where it reaches 1050 m. (3450 ft.). The lowest part of the boundary lies between the place where it crosses the Colorado River, at an elevation of 150 m. (490 ft.), and the place where it most nearly approaches the Salton Sea, at an elevation of 80 m. (260 ft.).

The boundary of the Sonoran Desert is most sharply defined geographically, as well as biologically, near the higher mountain ranges which it approaches in several places. The surface of the desert itself is essentially a series of slightly inclined plains on which are superposed innumerable hills and mountain masses, most of which are less than 915 m. (3000 ft.) in elevation. The percentages of surface occupied by mountain and plain vary in different parts of the area. The Pinal Mountains in Arizona and the Sierra Babiso in Sonora are the only ranges bearing mesic vegetation which are surrounded by desert.

The part of the Sonoran Desert north of the international boundary lies in the southern part of the Basin and Range Province, as defined by Fenneman (1928). It comprises most of the Sonoran Desert Section of this province, all of the Salton Trough Section, and a small part of the Mexican Highland Section. The part of the Desert lying in Sonora is a continuation of the Basin and Range Province, but Baja California is like southern California in its greater physiographic complexity.

The approximate area of the Sonoran Desert is 310,362 sq. km. (119,370 sq. mi.). This is divided among the four states as follows: Sonora, 126,256 sq. km. (48,560 sq. mi.); Arizona, 105,404 sq. km. (40,540 sq. mi.); Baja California, 62,670 sq. km. (24,104 sq. mi.); California, 16,031 sq. km. (6166 sq. mi.). The approximate lengths of shore line are as follows: Gulf coast of Sonora, 950 km. (590 mi.); Gulf coast of Baja California, 1480 km. (920 mi.); Pacific coast of

Baja California, 1370 km. (850 mi.). All parts of Baja California lie within 80 km. (50 mi.) of tidewater. Of the remaining part of the Sonoran Desert, approximately one-half lies within that distance of the Gulf of California.

Drainage Systems

The Gulf of California is the recipient of all the drainage of the Sonoran Desert except the small fraction that finds its way into the Pacific Ocean. Map 1, at the front of this volume, shows the principal rivers. The largest rivers rise outside the desert in the mountains of Colorado, Arizona, or Sonora, and cross the desert with diminishing volume and constancy. The only large enclosed basin is the Salton Sink, the bottom of which was 88 m. (287 ft.) below sea level before the formation of the present Salton Sea in 1905. There are a number of small undrained basins at low elevations in Arizona and Sonora, and in Baja California there is one in the interior, Laguna Seca Chapala, as well as a large number of shallow or poorly defined ones along the Pacific coast from Vizcaíno Bay to the Magdalena Plain. There are several large semi-bolsons, or nearly enclosed basins, in which a normal dendritic drainage system has developed but rarely carries floods great enough to discharge into its potential outlet. The only river with a perennial surface flow is the Colorado. Before the building of the Roosevelt and Coolidge Dams, the Gila River was a nearly constant stream. The other rivers which rise outside the desert show a seasonal variation in volume and in the distance to which their flood waters are carried after reaching the plains. The largest endogenous desert river is the Sonoyta, in northwestern Sonora; its floods are never discharged to tidewater. The Río Magdalena and Río Sonora rarely discharge their flood waters to the Gulf, but the Río Yaqui does so annually with almost unbroken regularity. The desert tributaries of the largest rivers, as well as the small independent streamways, are in flood for only a few days or even a few hours in the rainy seasons.

Despite the fact that the Colorado River is the largest and most constant stream traversing the Sonoran Desert, the influence of its waters on the vegetation of the desert is very restricted. It enters the desert 25 km. (15 mi.) north of Needles, California, where its mean level is 150 m. (490 ft.) above the sea. It falls at a nearly uniform rate from that place to the head of the Gulf, an airline distance of 358 km. (215 mi.). Parts of its meandering course are bordered by hills or cliffs of old river deposits, and parts by flats subject to inundation and covered with emergent swamp plants or forests of cottonwood. There are few places where the fringe of palustrine vegetation exceeds 3 km. in width.

On its right bank the Colorado receives only small and unimportant tributaries. On the left bank it is fed by the Bill Williams and Gila Rivers, as well as by several small washes. The Bill Williams River carries the drainage of the hilly and broken region between the east side of the Hualpai Mountains and the vicinity of Congress Junction, Arizona. The Gila River rises in the mountains of southwestern New Mexico and is fed on its right by several small rivers which drain the south face of the Colorado Plateau. Its most important tributary on

the left is the San Pedro River, which rises in northern Sonora. Whereas the flow of the Colorado is stabilized by the vast area of its distant head, that of the Gila is largely contributed by brief and heavy rainstorms falling near the margin of the desert.

The Río Sonoyta has its head in a large number of small washes which drain valleys in western Pima County, Arizona, and in the northern part of the District of Altar, Sonora. Most of its catchment basin lies between elevations of 500 and 600 m., and none of the small mountains draining into it exceeds 1000 m. It is therefore a river of strictly desert regimen. The upper tributaries converge toward a spot at which the river traverses a pass in the Sierra de Nariz, whence it flows west-northwest for 70 km. In the latter stretch the underflow is augmented by some springs east of the village of Sonoyta. Near the village of Quitovaquito the bed of the Sonoyta broadens and the river veers sharply to the southwest. At this place, known as the "Salada de Sonoyta" (see pl. 7), most of its floods terminate. The remainder of its course of 95 km. is through very arid plains. It has a well defined channel as far as the inner edge of the sand dunes which border the Gulf coast, but the flood waters, so far as is known, never penetrate the dunes to the Gulf. Ives (1936) has published a description of the Río Sonoyta and the behavior of its flood waters.

As one follows the Gulf coast of Sonora southward from the mouth of the Colorado, for the first 265 km. only a few small arroyos discharge to the Gulf. At the distance mentioned is the mouth of one of the important rivers of Sonora, which is designated at its head as the Río Babasac, and through its course in turn as the Río Magdalena, Río Ascensión, and Río de la Concepción. This system will herein be styled the Río Magdalena. It rises in grassy plains west of Cananea at an elevation above 1000 m. All the upper drainage flows through a narrow canyon 15 to 25 km. northeast of Ímuris. In the 55 km. between the canyon and Santa Ana, several small but well watered tributaries occur, and the broadening of the flood plain has favored agricultural development. At Santa Ana the Río Magdalena emerges onto the plains (at 680 m.) and changes in character from a river with nearly constant flow to a floodway of the desert type. Numerous small tributaries reach the river below Santa Ana, the most important being the Río Altar, which joins it just above the village of Pitiquito. With occasional exceptions, the summer floods extend down the Río Magdalena as far as Pitiquito or 16 km. farther to Caborca. In the remaining 120 km. of its course to the Gulf, the river has a fall of 330 m. and only one lowland tributary, the Arroyo Coyote. Only in seasons of very heavy rainfall does the Magdalena debouch into the Gulf.

South of the mouth of the Río Magdalena no important streams enter the Gulf for a distance of 225 km. At that point the Bahía de Kino receives the Río Sonora and several small intermittent streams. The Río Sonora rises within 40 km. of the international boundary in the grassland plains east of Cananea, and flows almost due south for 170 km. It then follows a southwesterly course as far as Hermosillo, emerging from low hills onto the desert plains just below Ures. Closely parallel to the upper course of the Río Sonora is the Río San Miguel,

running for a long distance about 50 km. west of the Río Sonora and flowing into it immediately above Hermosillo. Both the parent river and its principal tributary maintain a nearly constant flow to the point of junction. From Hermosillo the Río Sonora follows a west-southwesterly course to the Gulf, and in this section has only a seasonal flow of water. The gradient of the last 75 km. of the Río Sonora is much less than that of the Río Magdalena in its final stretch, and topographic evidence indicates that the former river has built a much larger deltaic plain than the latter.

South of Bahía de Kino the coast is again without important streamways for 190 km., to the point where the mouth of the Río Yaqui is found, now traversing the northern edge of the great delta which it has formed. The Río Yaqui is the most important river of Sonora, with its sources in southern Arizona and northwestern Chihuahua. It drains nearly all the western slope of the Sierra Madre Occidental north of latitude 28° N. Seen at the head of its delta in flood season it rivals the Colorado River in width and volume, but in the dry months its lower course may be without running water for several weeks. The most important tributaries of the Yaqui are the Moctezuma, the Bavispe, and the Haros. The upper course of the Haros is known as the Río Papigochic, and drains the east side of the Sierra Madre in Chihuahua for a distance of 100 km., as well as extensive grassland valleys east of the continental divide.

Mountain Ranges

The Sonoran Desert is hedged in by mountains which rise gently or abruptly from its borders except along the line of separation from the Mojave Desert between Needles and Indio, California, the line of separation from the Cape Region on the Pacific side of the tip of Baja California, and the line between desert and thorn forest in southern Sonora. The climatic influence of the surrounding mountains is important for the desert, and it has just been shown that the principal streamways of the desert are fed by the mountains. The desert itself is studded with mountains and hills, but, as was mentioned above, only two ranges are high enough to bear mesic vegetation: the Pinal Mountains of Arizona and the Sierra Babiso of Sonora. About 70 per cent of the area of the Sonoran Desert has the basin-and-range type of topography, giving the impression of a great plain on which the mountains rest. Elsewhere the entire surface is hilly or broken, with only narrow bands of level ground along the streams or coast. The latter type of surface extends along the inner edge of the desert from Needles to Quiriego, and covers about 80 per cent of the desert area in Baja California.

A trend from northwest to southeast is strongly marked in the mountains of Arizona and northwestern Sonora. In eastern Sonora the trend is nearly north and south. In Baja California the mountain axis of the peninsula has a northwest-southeast position, but there is great deviation from it in the smaller ranges of volcanic origin.

The writer has shown elsewhere (Shreve, 1922) that the upper limit of desert vegetation on mountains which rise from desert plains is strongly influenced by

the summit height of the mountains. The vegetation of the summit of a small mountain of 1500 to 1800 m. is composed of lowland desert plants and a few representatives of desert-grassland or encinal, whereas the same elevations on a large mountain of 2500 to 3000 m. are forested.

Among the mountains which lie wholly within the Sonoran Desert, the vast majority are of such low elevation that their summits are clothed solely by desert plants. There are, however, a number of small ranges which rise 700 to 1200 m. above the surrounding plains and furnish congenial habitats for plants that are common in the larger mountains just outside the desert, but are never or rarely found on the desert floor.

In Baja California the Sierra Juárez and Sierra San Pedro Mártir bear extensive areas of coniferous forest, and their eastern slopes fall abruptly to the very arid deltaic and coastal strip which connects the desert of California, Arizona, and Sonora with the desert part of Baja California. The very irregular series of mountains which forms the backbone of the peninsula rises in several localities to more than 1500 m., but in no case are there large areas above that elevation. The Sierra de Calamajué y San Luis lies between latitudes 29° and 29° 30′ N., and its rocky summits bear a few scattered oaks and junipers. The Sierra San Lino and the peak Las Tres Vírgenes have abrupt volcanic summits on which desert plants are dominant. In the Sierra de las Palmas and the Sierra de Zacatecas, which lie west of Bahía Concepción, the summits are better watered and have restricted areas of open xeric forest resembling that which covers most of the Cape Region.

The mountains in the Californian section of the Sonoran Desert and in the extreme southwestern part of Arizona appear at a short distance to be devoid of vegetation. They do, in fact, support an extremely open stand of highly xeric plants, which are not abundant enough to influence the color given the slopes by the bare rock. These mountains are often narrow and long, maintaining the same width for 100 km. or more, presenting a jagged crest which varies little in height, and meeting the desert bajadas or plains with great abruptness and at a remarkably uniform distance from the crest of the range. Mountains of this type, characteristic of the Basin and Range Province, are not encountered in Baja California (except in the Cucopah and Sierra Pinta ranges west of the Colorado Delta) or in the eastern half of the desert in Arizona and Sonora. Examples of this type of mountain are furnished by the Chocolate Mountains in California, the Mohawk and Sierra Pinta ranges in Arizona, and the Sierra Espuma and Sierra Basura in Sonora.

In the Basin and Range Province in Arizona and Sonora there are numerous mountains which depart widely from the elongated narrow form, often by reason of recent volcanism, but nevertheless have the characteristic highly dissected appearance, with sharp ridges separating the drainages and converging toward the summit. The volcanic mountains assume an infinite variety of forms, with extruded plugs or basaltic mesas contributing to their bizarre outlines. The abrupt walls, bare columns, and deep canyons found in small mountains of this

type are well developed in the Ajo, Castle Dome, and Kofa Mountains in Arizona and in the Sierra Picú in Sonora. See plates 9, 10.

Throughout the eastern half of the desert the mountains differ in size, elevation, orientation, and character of rock. The work of erosion has varied with the differences in resistance, and there is nowhere the uniformity of pattern that is so general in the topography of the flanks of the Basin and Range mountains.

Climate

A relatively uniform type of climate exists throughout the Sonoran Desert, with regional differences due to latitude, elevation, and the geographical configuration of the area. In spite of the nearness of the Pacific Ocean and the intrusion of the Gulf of California, the climate is distinctly of the continental type. This is particularly true of the northernmost part, which lies in the lee of high mountain ranges and is not influenced by the narrow waters of the head of the Gulf of California. Along the Pacific coast of Baja California desert vegetation exists with little modification up to the dunes and strand. The only climatic influences of the sea along the immediate coast are a slight lowering of the diurnal temperature, the intermittent effect of fog, and the almost constant blowing of a strong onshore wind. On the two coasts of the Gulf even these effects are absent except for a slight lowering of the sensible temperature within 100 m. of the shore during the daytime.

The difference of 11° of latitude between the northern and southern ends of the Sonoran Desert underlies a considerable difference between the winter temperatures in the north and south. As regards summer temperatures, the influence of latitude is outweighed by the more continental position of the northern end.

The gradual increase in elevation from the coasts to the interior results in a slight fall in the temperature range and brings the inner half of the desert within reach of occasional severe frosts. The same feature also causes a considerable increase of precipitation in the interior, further augmented by the mountain wall which forms the northern and eastern boundary.

Temperature

Parts of the Sonoran Desert share with Death Valley the highest and most sustained air temperatures in North America. Days with a maximum temperature of 90° or more occur exceptionally in February and may persist as late as December. Periods of 90 consecutive days with a maximum of 100° are not exceptional. There is no question as to the length of the growing season so far as temperature conditions are concerned, for there may be at least some vegetative activity in locally favorable spots throughout the year. The length of the frostless season ranges from 8 to 12 months in different parts of the desert. The duration of the potential growing season is interrupted by the rainless periods, which sharply reduce all plant activity.

In evaluating the effects of high temperature on plant and animal life, con-

sideration must be given to the accompanying dryness of the soil, the aridity of the air, and the long, cloudless days of strong insolation. Wind must also be considered a desiccating agent for plants, though many influences co-operate with it in extracting the last vestiges of moisture from leaves and stems. The days with highest sensible temperature and greatest desiccating effect are in June. The advent of the summer rains lowers the temperature range for a few hours or a few days, according to the duration of rainstorms and cloudiness. With the ending of the rains in September the high temperatures return, and late September and early October are usually as warm and dry as June.

The human reaction to a desert day was aptly expressed by Lumholtz, who stated that he felt as if he were "walking between two great fires."

In table 1 are shown the conventional temperature data for 8 stations in the Sonoran Desert: 3 in Arizona, 3 in Sonora, and 2 in Baja California. These figures show the well marked difference between the three Arizona stations, with their continental position, and the remaining stations situated on or near the coast of the Gulf of California. The Arizona stations show higher maxima in June, July, and August and lower minima during the winter months. The small differences in maxima and minima between Yuma, Phoenix, and Tucson are due to differences in elevation. Although Altar and Hermosillo are both at lower elevations than Tucson, they have lower maximum temperatures and higher minima than does Tucson. The lowest summer temperatures are found at Mulegé and La Paz, except in August and September at Mulegé. In general the monthly minima at Mulegé and La Paz are lower than at Guaymas and considerably higher than at the Arizona stations.

Rainfall

The amount and seasonal distribution of precipitation is the most important physical condition limiting the boundaries of the Sonoran Desert and is likewise the most important in determining the differences to be found in the various parts of that area. In regions of low rainfall the figures showing the monthly or annual totals, or even the averages for 10 or 15 years, have relatively little significance. In its importance for plants there is a wide difference between rain of a given amount in the cool months and in the hot ones. The upbuild of soil moisture effected by a brief torrential downpour is much less than that from a gradual rain of the same amount. Widely different effects are produced by a single rain of 50 mm. and five rains of 10 mm. each on successive days. A rain falling on a moist soil penetrates much more effectively than it would if the soil were dry. These considerations and a number of others make it inadvisable to place much emphasis on small differences in rainfall records for arid regions.

Of particular importance to plants are the number and duration of drought periods, which may be defined as periods without rain or with none of sufficient amount to affect the soil moisture. Such periods with a duration of 30 to 60 days are of almost annual occurrence in the Sonoran Desert. The large nonsucculent perennials are able to withstand them by drawing on the deep-seated moisture.

TABLE 1

AVERAGE MAXIMUM, MINIMUM, AND MEAN TEMPERATURES (IN DEGREES FAHRENHEIT) FOR 8 STATIONS IN THE SONORAN DESERT FOR THE YEARS INDICATED

MONTH	ARIZONA			SONORA			BAJA CALIFORNIA	
	Yuma 1878–1930	Phoenix 1896–1930	Tucson 1892–1928	Altar 1923–1938	Hermosillo 1923–1938	Guaymas 1923–1938	Mulegé 1923–1938	La Paz 1923–1938
MAXIMUM								
Jan.	66.7	65.0	65.2	61.9	63.3	72.3	60.3	66.0
Feb.	72.0	65.0	65.2	61.9	66.7	69.6	64.0	67.5
Mar.	78.1	74.1	73.4	65.1	73.0	74.7	69.4	72.1
Apr.	85.4	81.8	80.7	73.6	71.6	75.6	72.1	73.8
May	92.5	90.0	89.3	80.6	82.6	82.0	77.4	77.4
June	101.7	100.9	98.8	87.6	89.8	87.4	83.7	82.0
July	105.5	102.7	98.6	91.0	91.8	92.1	88.7	84.9
Aug.	104.1	100.9	96.8	89.8	89.4	88.3	90.5	86.2
Sept.	99.6	96.7	94.3	87.0	89.2	87.3	87.6	85.3
Oct.	88.0	85.9	85.1	78.6	....	83.5	80.4	80.8
Nov.	76.2	74.5	74.3	70.0	....	76.1	72.0	74.5
Dec.	67.2	65.0	64.9	64.6	....	69.8	61.7	69.3
Year	*86.4*	*83.9*	*82.4*	*76.1*	....	*79.5*	*75.6*	*76.6*
MINIMUM								
Jan.	42.2	38.7	34.3	49.5	58.3	60.1	53.8	61.9
Feb.	45.7	42.4	37.5	53.6	58.8	62.8	55.0	62.6
Mar.	49.6	46.7	41.3	56.7	62.0	65.8	60.1	64.4
Apr.	54.1	52.3	46.1	63.0	70.5	70.5	61.3	69.4
May	60.1	59.5	53.8	70.7	71.8	75.0	64.4	72.1
June	67.8	68.8	63.6	76.8	85.8	82.6	76.3	75.2
July	76.6	76.5	72.2	84.2	87.8	84.6	81.7	81.7
Aug.	76.2	75.3	70.6	83.3	87.1	84.0	79.0	80.0
Sept.	69.2	68.4	64.3	79.2	....	83.8	78.8	78.3
Oct.	57.5	55.6	51.6	69.1	....	78.8	69.8	77.2
Nov.	48.4	45.2	41.4	58.6	....	69.8	63.1	69.4
Dec.	42.8	38.5	35.2	53.4	....	63.1	53.2	64.4
Year	*57.5*	*55.7*	*51.0*	*66.6*	....	*73.4*	*66.4*	*71.4*
MEAN								
Jan.	54.3	50.9	49.7	55.0	60.3	63.9	57.2	64.1
Feb.	58.9	55.1	49.7	59.5	63.1	66.0	60.8	64.9
Mar.	63.9	60.5	57.3	61.7	68.0	69.3	64.0	69.1
Apr.	69.8	67.1	63.4	68.0	73.6	73.0	68.2	71.2
May	76.3	74.7	71.5	75.7	79.5	77.9	73.2	74.5
June	84.7	84.4	81.2	83.7	87.8	83.8	80.9	78.1
July	91.1	89.7	85.4	88.5	89.6	87.3	86.9	82.7
Aug.	90.3	88.4	83.7	86.7	88.5	86.9	86.7	84.0
Sept.	84.4	82.0	79.3	84.0	86.4	86.4	84.2	82.9
Oct.	72.7	70.3	68.3	74.1	....	81.1	76.3	79.0
Nov.	62.3	59.2	57.8	64.0	....	72.7	67.1	72.7
Dec.	55.2	51.9	49.9	57.5	....	65.5	58.8	66.4
Year	*72.0*	*69.5*	*66.6*	*71.4*	....	*76.1*	*72.0*	*73.9*

In soils of fine texture the moisture at a depth of 2 m. is nearly constant throughout the year and is affected from year to year only by very exceptional periods of drought or rain.

The writer has published (Shreve, 1934) a digest of the rainfall, runoff, and soil-moisture records of the Desert Laboratory at Tucson. These data serve to illustrate many features of the rainfall which are characteristic of the entire Sonoran Desert.

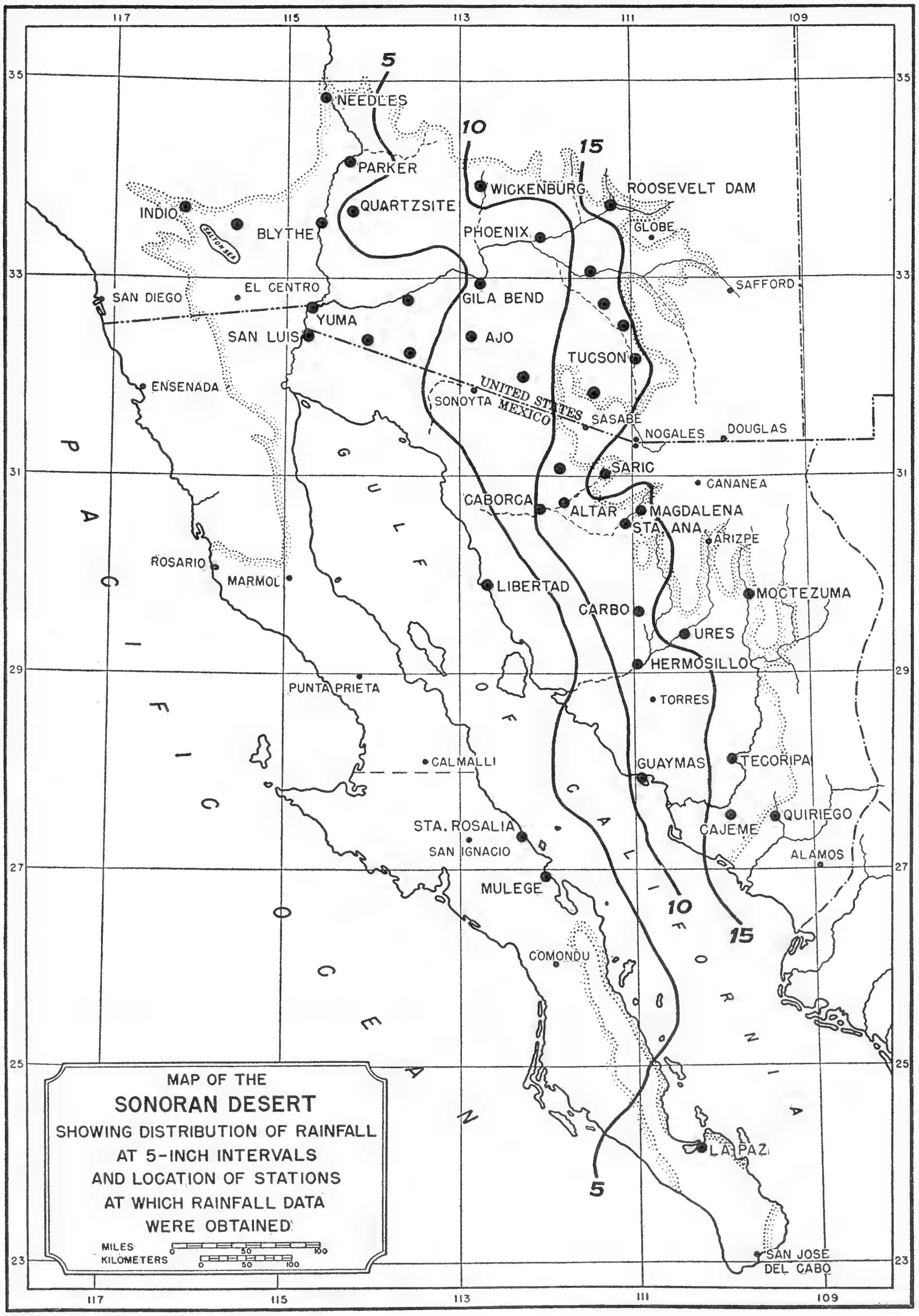
An important feature of rainfall in the Sonoran Desert is the change in seasonal distribution which is encountered on going inland from the Pacific coast. West of the drainage divide of Baja California and north of Mulegé, rain is confined to the late winter and early spring. Winter rain forms about 50 per cent of the annual total at Yuma and 40 per cent at Altar. At Tucson the winter and summer rains are nearly equal, and 80 km. farther east, at Benson, Arizona, the winter rain decreases to 25 per cent. The sporadic summer rains of the Gulf coast of Baja California increase to 20 per cent of the annual total at Yuma, to 35 per cent at Gila Bend, and to 50 per cent at Tucson; in Sonora, the percentage at Altar is 66 and at Guaymas 72. There are further increases in the percentage for the summer months in the eastern valleys of Sonora and in southern Sonora and Sinaloa.

The winter period of precipitation extends from December to the end of March or the middle of April. The summer period is sharply limited to July, August, and early September. The winter rains are gentle and prolonged and usually occur over wide areas. The summer rains are commonly brief and torrential and limited to paths or small areas.

The accompanying map (map 3) of rainfall distribution is based on data for 4 stations in California, 17 in Arizona, 16 in Sonora, and 3 in Baja California. The map is purely provisional, as the records vary in length and reliability and considerable interpolation has been necessary. The outstanding feature is the gradual increase from readings of 55 mm. at San Luis, Sonora and 79 mm. at Yuma, Arizona to 459 mm. at Roosevelt Dam, Arizona, 443 at Saric, Sonora, 469 at Moctezuma, and 445 at Tecoripa. It is also noteworthy that most of the stations in northern Sonora have higher rainfall than do Arizona stations located at elevations 300 to 400 m. higher. In northern Sonora the distance from tidewater to the Sierra Madre mountains is great, but in southern Sonora the coastal plain narrows to less than 150 km. This is an important factor in increasing the rainfall of the inner edge of the coastal plain and in determining the southern boundary of the Sonoran Desert. Humphrey has given a detailed account of rainfall in this and other deserts (1933).

Soils

The origin, mode of formation, and developmental history of soils in a desert region present many features which are common to all soils, at the same time that they exhibit a number of distinctive phenomena and conditions which are to be attributed to the deficiency of rainfall or else to its intermittent and torrential character.



MAP 3. Distribution of rainfall at 5-inch intervals. Large dots indicate location of stations at which rainfall data were obtained.

The basic importance of the underlying rock in determining the character of residual soils is as great in the desert as it is elsewhere. The arid climate begins to exert its influence, however, in the very genesis of soil formation, in the weathering of rock in place and the disintegration of rock fragments. In the Sonoran Desert the influence of frost in weathering is negligible. It seems possible that disintegrating action may be exerted on black and very dark-brown basaltic rocks by the sudden falling of rain at a time when the rocks are hot. The first water which falls on them is so greatly heated that its power as a solvent is far greater than that of cold rain water. Rocks with a surface temperature of 150° to 160° F. are often suddenly bathed by rain water with a temperature of 60° to 70°, and the sudden and great temperature changes to which they are thus subjected must do much to aid in the disintegration of the less resistant rocks.

The decomposition of rock fragments and the coarser soil elements, as distinguished from their mechanical disintegration, is accomplished slowly in arid climates as compared with humid ones. This results in the formation of soils which vary in the mineralogical character of the smaller particles, and include many small particles of composite nature.

The disintegration of rock surfaces by wind-borne sand is sometimes locally of greater extent than the weathering due to water. Small hills and isolated rocks lying near the general level of large plains are more subject to wind erosion than are the slopes of larger hills or mountains. Even the very small rock fragments which cover the surface of the ground are worn slowly by shifting sand. Where there is an abundance of fine, loose material, it is often actively moved along the surface of the ground when the wind is not strong enough to raise visible clouds of dust. The cutting action of the sand blast cannot always be gauged by the number of dust storms which occur. Large bodies of shifting sand are found in numerous areas around the head of the Gulf of California. Though there are only a few localities which show conspicuous evidence of wind erosion, the phenomenon is going on to a slight extent throughout the sandy part of the Sonoran Desert.

The general features of the relation of land forms and physiographic processes to soil history are the same in arid and in humid climates. A series of soils ranging from mountain side or talus slope through outwash slope and bajada to playa or flood plain will exhibit a decreasing number of large stones and an increasingly finer texture. Because of torrential rains and the lack of a continuous cover of vegetation, there is a more ready downgrade movement of coarse material in the arid climate, and a consequent coarser texture in the soils of such relatively mature surfaces as the lower bajadas.

McGee (1897) has described the manner in which the runoff takes place over a bajada following a torrential rain. Water flows in a continuous sheet over areas of hundreds of acres, to a depth of 1 cm. or more, rapidly replaced by the precipitation and the drainage from up slope. The cutting of the surface by such drainage has been designated by McGee as "sheetflood erosion." Although there

has been some skepticism as to the occurrence of such a phenomenon, the writer can vouch for having witnessed it many times. The sheets of water are of local occurrence and of very brief duration, but there must be very few appropriate areas in the desert that are not visited by them once or twice every year. After the cessation or onward movement of the rain, the sheet of water vanishes from the general surface. The smallest streamways are filled with water for a few minutes longer. The larger streamways, from 1 to 2 m. wide, are in flood for 10 to 20 minutes. Thirty minutes after the cessation of the rain, no free water surfaces are to be found except in the largest streamways.

It is erosion of the type just described that does more than any other one factor to give the bajadas their characteristic uniformity of gradient and their consequent straight-line profiles. This is also the principal factor in the removal of the finest material from the surface and its transportation to playa or flood plain, and it is further the means of removal of leaves, small twigs, fruits, feces, and other materials which serve to build up the organic content of soils in which they find a resting place.

Tolman (1909) contends that such floods constitute "in every case a depositing and not an eroding sheet, save when confined to a valley where it can do some undercutting." A detailed investigation of sheet floods would undoubtedly show that their behavior is in many respects analogous to that of streams. They are merely streams of very intermittent character and slight depth which are not confined to definite banks. The ratio between the erosional and the depositional work which they perform is a function of the character of the surface over which they move, the gradient of the surface, and the load which the sheet is carrying. The movement of such sheets brings the water rapidly into depressions and normal drainageways. The observations of the writer would indicate that the sheet is the stage of most active erosion, and that the rapidly succeeding movement of the flood waters in the streamways or over the flood plains or playas is the stage of greatest deposition.

The removal of the finest soil material leaves a surface covered with rock fragments in a great variety of sizes, depending upon the location. Near localities where there is rock in place the surface fragments are larger and more numerous, and they decrease in size and abundance on passing toward the playas and flood plains. In all but the finest types of desert soils the surface gives the impression that the soil has a much coarser texture than is actually the case. Beneath a surface which is almost completely covered with stones from a few millimeters to several centimeters in diameter will be found a fine-textured soil, often containing a surprisingly low percentage of such coarse material as covers the surface. The distance to which the surface fragments have been transported is often small, and their form is almost invariably angular. Having accumulated on the surface as a result of violent precipitation, these coarse fragments serve as a protection against the impact of rain and the cutting power of the sheet floods. In general, wind plays a minor role in the removal of fine surface material. Some of it is moved from place to place, but it never accumulates after the manner of sand.

The close-set surface covering of small stones has been called "desert pavement," "erosion pavement," or "lag gravel." In some localities its surface has been long undisturbed and slowly worn down to a uniform level by wind erosion. See plate 1; plate 2, figure 1.

A very constant distinguishing feature of desert soils is the low content of organic matter and the consequent small percentages of humus. Primarily this condition is due to the thinness of the plant cover and the small amount of falling and decaying vegetable matter. Sheet floods wash away much of the small plant litter and deposit it in the playas and flood plains. Such organic matter as the soil contains is rapidly oxidized and decomposed, with the consequence that the humus content is low, even in the flood plains, as compared with that of the soils of humid regions. Figures given by Hilgard (1906) show the amounts of humus in soils of the Colorado and Mojave Deserts of California to range from 0.25 to 0.65 per cent, as compared with a range from 3 to 5 per cent in soils of humid regions. To the poverty in organic matter may be attributed in part the light color and hard surface of most desert soils, as well as the absence of any criteria for distinguishing soil and subsoil.

From the reciprocal relation between the water content and the air content of soils, it follows obviously that arid soils are well aerated most of the time. With the prevailingly thin water films that accompany the dry states of the soil, there is nearly the maximum air content for the given type of soil, and good air communication to a depth which probably exceeds that of plant roots. Though such conditions prevail most of the time over most of the desert, however, there are sometimes local conditions which bring about very poor soil aeration. In the flood plains, and more particularly in the poorly drained playas, the flood waters of the rainy seasons may accumulate to such a depth immediately after the rains as to saturate the soil and to keep it in this condition for a number of days. The harmful effect of the saturation may go so far as to kill trees 30 to 50 years old.

The most striking and best-known peculiarity of desert soils is their high content of readily soluble salts. The accumulation of these is very obviously due to the limited extent to which rainfall has been able to bring such salts into solution and to carry them through a constant series of streams to the sea. The existence of many bolsons and semi-bolsons means that flood waters are held and subjected to evaporation near their place of origin, with resulting heavy accumulation of salts in their playas. Some of the largest streams of the Sonoran Desert are unable to carry their heavy loads of alluvium and dissolved salts through to the sea. Also, much of the precipitation which falls on desert soils is destined to penetrate them to a short distance, dissolving the salts present, and then to return to the surface on account of the active evaporation, depositing the dissolved salts again in almost the precise spot which they originally occupied.

The extended comparisons of arid and humid soils made by Hilgard show that the most constant and striking difference lies in the high calcium content of desert soils, with high magnesium content somewhat less important. In the Sonoran Desert the commonest soluble or somewhat soluble salts in the soils are the carbonates, chlorides, and sulfates of calcium, magnesium, and sodium.

Closely associated with the high salt content of desert soils is the occurrence of superficial incrustations or of buried layers of hardpan. In alluvial soils which become very wet at certain seasons, and also in soils which have been irrigated for many years, there may often be found a thin but conspicuous layer of salts uniformly covering the irregularities of the surface. These incrustations are usually white, but are black where there is a high proportion of sodium carbonate in the soil solution, owing to the action of the carbonate on the organic matter of the soil. The layers of hardpan, better known by the widely used Spanish name *caliche*, are of wide occurrence in the North American deserts in certain types of soil and in certain topographic situations. The caliche consists of hard white sheets or layers from a few millimeters to 10 cm. or more in thickness and sometimes as much as 10 to 15 sq. m. in area, or elsewhere serving to cement together the stones and rocks of the subsoil in a discontinuous layer. Caliche may lie near the surface, or may even be exposed in localities where the surface has been actively eroded; on the other hand, the uppermost layers may be as much as 2 m. below the surface, or rarely even deeper. In the localities where caliche reaches its greatest development it occurs in successive layers to a depth of over 30 m., there being from ten to twenty layers to a meter.

Some of the physical properties of caliche have been investigated by Shreve and Mallery (1933), with particular reference to its role in modifying the water relations of the soil and thereby influencing those of the plant. Their work indicates that caliche retards penetration of water and interferes with the development of the root system to an extent which outweighs its influence in retarding soil evaporation. Both experimental and field evidence indicate that its presence hinders the best development of desert vegetation.

3

Perennial Vegetation

General Characteristics of Deserts

The deserts of the world are as varied in their features as the forests are. Their plants differ in appearance, structure, behavior, and relationships. The feature that is common to all deserts is the limitation that is placed upon plants by an inadequate or uncertain water supply and by all the characteristics of climate, soil, topography, and drainage that are due to a low rainfall or associated with it. The limitation to which desert plants are subjected affects the number of plants per hectare, the size and height of the plants, the number of species per square kilometer, the number of growing days and total growth per year, the size of the seed crop, the opportunities for germination, and the chances for survival of seedlings, as well as the operation of all the processes concerned in evolution.

There is no single criterion by which desert may be recognized and defined in either the geographical or the biological sense. The amount of rainfall coincident with desert varies with temperature and the seasonal distribution of the rain. A true characterization of desert must include evaluation of many variables. It is essentially a region of low and unevenly distributed rainfall, low humidity, high air temperatures with great daily and seasonal ranges, very high surface soil temperatures, strong wind, soil with low organic content and high content of mineral salts, violent erosional work by water and wind, sporadic flow of streams, and poor development of normal dendritic drainage.

From the biological standpoint desert is best defined in terms of the limitations which have just been mentioned. For plants these serve to prevent the full degree of development that would enable them to form a closed covering, attain a considerable size, maintain vegetative activity throughout the year, and meet the environmental conditions without structural features or types of physiological behavior that tend to reduce their maximum performance.

The comparisons of plant life which are an essential feature of the study of its geographical relationships involve three aspects. These concern (*a*) the individual species with reference to its structure and physiological behavior; (*b*) the individual species with reference to its phylogenetic relationship; and (*c*) the communities with reference to their appearance, structure, relationships, environmental requirements, and composition. Examination of these aspects of desert vegetation shows it to have distinctive features in each of them. In greater or less degree, it differs from the vegetation of related regions in its life forms, in its genera and species, and in the character of its communities.

Types of Plants

Certain outstanding types of plants were recognized by the earliest plant geographers as playing an important role in the appearance of the vegetation and contributing to the character of natural landscapes. The occurrence of broad-leaved evergreen trees, palms, century plants, or bamboos was seen to have an important part in determining the general aspect or physiognomy of the vegetation. In later years the study of such types, called life forms or growth forms, has attracted the attention of a large number of plant geographers, and several detailed schemes for their classification have been proposed. A summary of the work in this field, with citation of important papers, has been given by Rübel (1920). Both the earlier and the later classifications of life forms are based upon obvious features of outward appearance, although the ultimate subdivisions begin to be colored by knowledge of the structure and relationship of plants.

Recognition of the outstanding life forms serves a useful purpose in descriptive plant geography. It will be a long time before we have a broad knowledge of the ecological equivalence of unrelated species of the same life form, or the differences in physiological behavior which may distinguish the unlike types. In view of these limitations there is no ground for multiplying the number of life forms beyond the needs of descriptive plant geography or beyond those subdivisions which have an obvious relation to the state of adjustment existing between the plant and its environment.

Consideration of the outstanding life forms is of particular importance in the discussion of deserts, with respect both to the physiognomy of desert vegetation and to the relation of the dominant plants to their environment. The mingling of dissimilar life forms throughout the vegetation is a characteristic of all but the coldest or most arid deserts. It is, in fact, a circumstance which seems to have considerable significance in the constitution of the vegetation of certain deserts. If the great nondesert plant formations of the world are compared, it will be noted that each of them is dominated by plants which are of the same life form, however widely they may differ in phylogenetic relationship. Tropical rain forests are dominated by evergreen broad-leaved trees, temperate rainy regions by deciduous broad-leaved trees, cold regions by needle-leaved evergreen trees, regions with light winter rain by broad-leaved sclerophyllous shrubs, and regions with low but well distributed rainfall by grasses. In each of these regions the conditions for plants are favorable and the competition between individuals, species, and life forms has been keen, resulting in the development of a high degree of uniformity among the dominant plants. In arid regions there has been much less competition. The greatest "struggle" of the plants has not been with one another, but with the environment. Therefore the conditions tending toward the elimination of certain types and the survival and dominance of a relatively uniform one have not been operative. This fact has brought about the diversity of plant types which characterizes many semiarid and arid regions and some extremely arid ones. The opportunity which the desert has offered

for the persistence of unstandardized types has undoubtedly resulted in the survival in it of species, and even of genera, for very long periods of geological time.

Species of Plants

Each of the great desert regions of the world has a flora which is distinct from that of adjacent moister regions. Despite the invariable overlapping of ranges along the edge of the desert, and the occurrence of widely distributed aquatic and palustrine plants around oases and along artificial streams, the true desert flora remains distinct and rather strictly confined to its own region. This is, indeed, only a detail of the broader fact that all the great plant formations of the world, distinguished by reason of their unlike vegetation, are also strongly unlike in flora.

The extremely arid deserts, as well as those that are high and cold, have a small flora. As more and more favorable deserts are examined, the flora is found to grow larger and larger. In the richest deserts the size of the flora is to be attributed in part to the relatively favorable conditions of moisture and temperature and in part to historical factors. It is in the deserts with the most favorable conditions and the largest flora that distinctive desert genera are found, and also a very small number of families which are wholly or almost wholly confined to the desert.

The conditions of the desert not only have influenced the vegetative structures of plants, but also have shaped the processes of evolutionary development, the origins, survivals, changes, and movements by which the present flora and its distribution have been determined.

Communities of Plants

The plant communities of the desert have some distinctive features and some which they share with the vegetation of other regions. The outstanding characteristics of most desert communities are the low but unequal stature of the plants, the openness of stand, and the mixture of dissimilar life forms. These features interact in some respects; for example, the inequality of stature is largely due to the mingling of life forms.

From these three primary features of desert communities arise others which are of importance. The low stature is responsible for the scarcity of truly subordinate plants, such as the secondary trees, undershrubs, herbaceous perennials, epiphytes, and lianes which are involved in the layering of the tropical rain forest. The openness gives ample opportunity for the establishment of new individuals of the dominant species or for invasion by other species, but it is an opportunity which is rarely embraced. The lowness and openness combine to cause a relative scarcity of plant litter. The little that is produced is to a great extent eaten by termites and only to a very small extent reduced by fungi and bacteria. By the added agency of winds and sheet floods the plant litter is prevented from permanently enriching the spot where it falls, and ultimately comes to rest on flood

plains and along streamways. Consequently this most important of the reactions of plants upon their habitats is reduced to a minimum in the desert. The long existence of a community in a given spot does little if anything to pave the way for the entrance of plants with life requirements different from those of the occupants.

Throughout the North American desert the character of the soil is of primary importance in determining the make-up and distribution of communities. The physical texture of the soil, its depth, and the nature of its surface are equally important. Less important, except in extreme cases, is the salt content. The profound influence of soil upon desert vegetation is to be attributed to its strong control of the amount, availability, and continuity of the water supply. This fundamental requisite of plants is the most effective single factor in the differentiation of desert communities.

The desert is often alluded to as being built on a vaster scale than other types of country. This notion is due to the untrammeled vision which its low vegetation permits. The long vistas of the desert make it easy to observe the uniformity of the plant cover, spread with little variation for long distances over terrain in which the soil is highly uniform. The frequency in the desert of extensive communities which are simple in composition is not due to the poverty of the perennial flora so much as to the severity of the physical conditions. In a given region there are few species able to persist in the least favorable habitats, which are invariably the ones with simplest floristic composition. Close to such habitats, in others of nearly identical climate but different soil, grow numerous other species whose presence is made possible by slightly more favorable conditions. In such simple communities the presence or absence of a particular species, or a change in its relative abundance, becomes important in determining the physiognomy. There are virtually no uncommon plants, except outlying individuals of the dominants of adjacent desert regions. The same few species occur over and over again, and the recurrence of a particular habitat brings a repetition of its characteristic community.

The successional changes which are so important elsewhere may be read into the vegetation of the desert, but the evidence for them would hardly suggest that they are of importance in determining the relations of the communities to one another. The secular changes of surface are accompanied by the shifting of the communities over long periods, by which their locations and areas are changed in the simplest possible manner. If a particular community is destroyed without change in the soil, the earliest stage in the return of vegetation will be the appearance of young plants of the former dominants. Not only do the same species reappear at the outset, but their first individuals ultimately constitute the restored community.

It is not possible to use the term "climax" with reference to desert vegetation. Each habitat in each subdivision of a desert area has its own climax, which must be given an elastic definition and must not be interpreted as having a genetic relation to any other climax. It is merely the particular group of species which,

in somewhat definite proportions and with a fairly definite communal arrangement, is able to occupy a particular location under its present environmental conditions.

Analogy with moist regions makes it natural to regard the vegetation of flood plains or river bottoms as the climax of desert regions. This is merely a case in which the plants of highest water requirement are occupying the habitats which have the most liberal water supply. The flood plain is the ultimate feature in the idealized course of physiographic development. At any given period in the history of a desert area the processes of degradation and leveling give a much greater area of upland, with far poorer water supply, and the vegetation of these areas might much more appropriately be regarded as the climax if it seems mandatory that the vegetation be interpreted in terms of physiographic processes. From a purely vegetational standpoint, on the other hand, the true climax that has been achieved by plants in clothing the desert is to be found in the richly diversified communities living in relatively favorable but purely desert environments, in which the plants exemplify the most advanced types of structure and behavior that have been developed to meet desert conditions.

The North American Desert and Its Parts

A nearly continuous arid region extends through western North America from the valley of the Snake River, in eastern Washington, southward and eastward to the Mexican state of Puebla. This irregular area of over 192,000 sq. km. (69,000 sq. mi.) is mainly continental and separated from the Pacific Ocean or the Gulf of Mexico by mountain ranges. Only in northwestern Mexico, in the state of Sonora and the territory of Baja California, does any part of the region lie at low elevations along the coast. Throughout its extreme length of 3700 km. (2300 mi.) there is to be found the characteristic groundwork of physical and biological features which distinguishes all desert regions. There are great differences, however, in the plant and animal life of the various parts of the North American Desert. With an extent of 27° of latitude, a range of elevation from sea level to 1525 m. (5000 ft.), and the attendant differences in climate, soil, and proximity to the sea, a complex background has been furnished on which plants and animals have followed diverse lines of development and have built up communities of wide variety.

With respect to the character of its vegetation, the North American Desert falls naturally into four areas. Following geographical and biological usage, these are designated Chihuahuan Desert, Great Basin Desert, Mojave Desert, and Sonoran Desert. The first is isolated, but the other three lie in a continuous series. Without regard to their individual features of geologic structure, physiographic development, and climate, the four deserts may be distinguished solely on the basis of their vegetation. The boundaries may be placed with varying degrees of definiteness, depending upon the sharpness with which the controlling conditions for desert and for adjacent types of vegetation meet under the alternation of mountain, plain, and plateau.

The Chihuahuan Desert

The North American Desert is divided, like that of South America, into eastern and western sections separated by the highlands of the continental divide. Between the northern ends of the Chihuahuan and Sonoran Deserts is the lowest part of the continental divide in its whole extent from the Peace River, in Canada, to the Isthmus of Tehuantepec, in southern Mexico. In extreme southeastern Arizona and southwestern New Mexico the separating region is a high plain, studded with small mountains, on which the conditions are arid but not desert and the vegetation is a transition between desert and grassland. Farther south the separation is more completely brought about by the Sierra Madre Occidental and its adjacent foothills and plateaus. Whereas the ranges of many desert plants extend across the lowest part of the divide, with or without interruption, there is a much more effective separation of the Chihuahuan and Sonoran Deserts south of the international boundary.

The Chihuahuan Desert comprises small areas in New Mexico and Texas, the lowlands of the Mexican states of Chihuahua and Coahuila, and parts of Durango, Zacatecas, Nuevo Leon, and San Luis Potosí. The vegetation of the Mexican deserts south of latitude 25° is best known through a publication of Ochoterena (1937), but this area has not been compared with the deserts of northern Mexico in sufficient detail to confirm fully the strong indications of Ochoterena's work that it constitutes a wholly distinct fifth desert region.

The Chihuahuan Desert lies mainly above 1070 m. (3500 ft.). Its precipitation ranges from 70 to 500 mm. (3 to 20 in.), of which 70 to 80 per cent falls between the middle of June and the middle of September. Its winter temperatures are low, with occasional periods of 30 to 72 hours of freezing temperature. The prevailing plants in the most widespread communities are low shrubs (*Larrea tridentata*, *Acacia cymbispina*, *Flourensia cernua*, *Prosopis juliflora* var. *Torreyana* as a shrub) or low leaf succulents (*Agave lechuguilla*, *A. falcata*, *Hechtia* sp.). Trees are found only along the drainageways, and tall cacti are represented only by infrequent cylindropuntias (*Opuntia imbricata*, *O. Kleiniae*). The most abundant low stem succulents are *Euphorbia antisyphilitica* and numerous species of *Echinocactus*, *Echinocereus*, *Coryphantha*, *Mammillaria*, *Escobaria*, *Thelocactus*, and *Neolloydia*. Semisucculents are the commonest tall plants, being represented by several species of *Yucca* (*Y. elata*, *Y. macrocarpa*, *Y. Treculeana*, *Y. carnerosana*, and *Y. australis*). The region is essentially one in which the dominance is shared by microphyllous shrubs and low stem succulents or tall semisucculents.

The Great Basin Desert

This northernmost part of the North American Desert is nearly coincident with the states of Nevada and Utah, with a slender extension into Oregon and Washington. Numerous mountain ranges are scattered over the Great Basin, most of which have either a xeric or a mesic forest cover, while the network of desert occupies the floors of the detrital valleys. The elevation lies above

1200 m. (4000 ft.) except in the extreme north. The precipitation in several localities is higher than in any other part of the North American Desert, but for the Great Basin as a whole it ranges from 100 to 270 mm. (4 to 11 in.), of which about 60 per cent falls in the winter months. The winter temperatures are sometimes very low and the frost periods long.

The vegetation of the Great Basin Desert is dominated by a small number of species of low shrubs, most of which are either wholly or partly deciduous. It is almost devoid of trees and also of shrubs with large evergreen leaves, and is poor in succulents and semisucculents. A distinctive feature of the vegetation is the predominance of communities which are very simple in composition or have as much as 95 per cent of their stand made up of a single species. The commonest dominants of these uniform communities are *Atriplex confertifolia*, *Artemisia tridentata*, *A. nova*, *Chrysothamnus puberulus*, and *Eurotia lanata*. Each of the communities is sharply confined to its particular site and type of soil, and in each of them the stature of the plants is determined by local conditions of water supply. In the simplicity of its vegetation and the small number of life forms it contains, the Great Basin Desert is distinctly of the cold northern type.

The Mojave Desert

The Mojave Desert lies in interior southern California and extreme southern Nevada, and is the smallest of the divisions of the North American Desert. Its elevation falls from 1200 m. (4000 ft.) on the western edge nearly to sea level at the Colorado River. The precipitation decreases from 125 mm. (5 in.) on the west to less than 50 mm. (2 in.) on the east, and occurs only in the late winter. Temperature conditions vary with altitude, so that only the western half is subjected to severe frost.

The Mojave Desert shows its most distinctive development between 600 and 1200 m. elevation (2000 to 4000 ft.). When it is followed thence toward the northeast or southeast, it loses some of its characteristic vegetational features and much of its distinctive flora. The groundwork of the vegetation throughout the Mojave Desert is a very open stand of *Larrea tridentata* and *Franseria dumosa*. On the western edge these plants are joined, and to some extent replaced, by *Artemisia*, *Chrysothamnus*, *Grayia*, *Tetradymia*, *Haplopappus*, and other suffrutescent perennials, and at higher elevations on the north *Coleogyne ramosissima* and *Grayia spinosa* are dominant. The only plants which rise above the low and open shrubbery are *Yucca schidigera* and *Y. brevifolia*, both of which are limited to the higher marginal elevations. Most of the Mojave Desert is very poor in succulents, and only on coarse detrital slopes along its southern and western edges will *Opuntia echinocarpa*, *O. basilaris*, and *Ferocactus acanthodes* be found in great enough abundance to affect the aspect of the vegetation.

The Sonoran Desert

The Sonoran Desert occupies the region in the United States and Mexico which surrounds the upper two-thirds of the Gulf of California. Its elevations

range from sea level to 1050 m. (3450 ft.). Its precipitation ranges from almost nothing to 330 mm. (13 in.) on its eastern edge, occurring only in winter on the western half and in winter and summer on the eastern. The winter temperatures are very mild in the south, with short freezing periods in the north.

The Sonoran Desert exceeds the other three deserts in the number and variety of its life forms and in the diversity of its plant communities. On the Pacific coast of Baja California low microphyllous shrubs, the leaf succulents *Agave* and *Dudleya*, several species of stem succulents, and the semisucculent *Yucca valida* are the dominant plants. In the interior, the higher areas support only low, dense stands of microphyllous shrubs, whereas the vegetation of the lower parts exhibits an unrivaled wealth in which nearly all the life forms found in the North American Desert are represented. At the low elevations along the lower Colorado River and the head of the Gulf of California the vegetation is low, open, and simple in composition, some of it being equaled in these respects only by some of the large bolsones of the Chihuahuan Desert. Above 300 m. (1000 ft.) in Arizona and northern Sonora the communities again become richer and more diversified, with many small trees and a strong representation of cacti of many types. In central and southern Sonora trees, shrubs, cacti, and sarcophytes are represented in nearly all the communities. The density is very irregular, but in some communities of shrubs and small trees there is nearly complete coverage.

Contrasting Features of the Four Deserts

The salient differences in the vegetation of the four divisions of the North American Desert are closely correlated with their differences in geographical position, in elevation, and in climate. These groups of physical conditions are strong in their operation even where they are not sharply delimited in area.

The very brief descriptions of the four areas which have just been given are sufficient to support the view that the Sonoran Desert is by far the richest in number of life forms and in variety and development of communities. It has large numbers of both evergreen and deciduous shrubs with a wide range of leaf sizes. It has many species of small trees which mingle with the shrubbery on the open plains and include both highly xeric and somewhat mesic types. It supports a display of succulents of great variety in form and size, as well as leaf succulents, semisucculents, and sarcophytes. Its flora is enriched by two large groups of ephemeral plants which appear separately in the two rainy seasons. The wealth of life forms found in the Sonoran Desert is reduced in number and in physiognomic importance on passing north or east into the other deserts. Lower rainfall, limitation of rain to a single season, and lower winter temperatures are the principal factors involved.

The small trees which form the arboreal deserts of Sonora and Baja California are confined to the Sonoran Desert. The most important of these trees are: *Cercidium microphyllum*, *C. floridum*, *C. sonorae*, *Olneya tesota*, *Jatropha cinerea*, *J. cardiophylla*, *Bursera microphylla*, *B. Hindsiana*, *B. filicifolia*, *Pachycormus*

discolor, *Pithecellobium sonorae*, and *Ipomoea arborescens*. Some of the trees confined to streamways or alluvial plains in the Sonoran Desert are also found in the other deserts. Among these are *Prosopis juliflora* var. *Torreyana*, *Populus Fremontii*, *Sapindus Saponaria* var. *Drummondii*, *Chilopsis linearis*, and *Celtis reticulata*. A large number of leguminous trees which are not of xeric stamp are characteristic of lower elevations in the Sonoran Desert, including *Acacia occidentalis*, *A. Farnesiana*, *Caesalpinia pumila*, *Lysiloma candida*, *L. Watsoni*, *L. divaricata*, *Eysenhardtia orthocarpa*, *Erythrina flabelliformis*, and *Mimosa laxiflora*. None of these reach the Mojave or the Great Basin, and the only upland trees of this type in the Chihuahuan Desert are *Acacia Farnesiana* and *A. Berlandieri*. In general the arborescent habit is indicative of favorable moisture conditions. In the Sonoran Desert trees are favored as much by the biseasonal occurrence of rain as by its amount. The Mojave and Great Basin are dry during the season of favorable temperatures, and the only arboreal form suited to such conditions is *Yucca brevifolia*.

The number of species of evergreen shrubs in the Sonoran Desert is not large, but they include the ubiquitous *Larrea* as well as *Simmondsia chinensis*, *Condalia spathulata*, *Celtis pallida*, *Cordia sonorae*, *Sapium biloculare*, *Atamisquea emarginata*, and *Viscainoa geniculata*. The evergreen habit is indicative of the ability of the plant to carry on its leaf functions not only during the cold months, but during the dry ones as well. The region of mild, rainy winters is the one to which nearly all the desert evergreens are confined. *Larrea* is able to range from this favorable region into parts of the colder Mojave Desert as well as into the Chihuahuan Desert, where the winter rain is very light. It is not able to endure the winter temperatures of the Great Basin Desert. The wide range of this shrub in the drier and somewhat colder deserts may be due to its being a facultative evergreen, sometimes losing four-fifths of its leaf surface in very dry periods. Thus enabled to endure the rainless summers of the Mojave Desert, it finds its most favorable season in the late winter and early spring.

The native American succulents are immune to long seasons of drought, but require favorable periods for the replenishment of the water content of their tissues. In the region of biseasonal rainfall, replenishment is greater in the summer than in the winter, being slight during periods of low soil temperature. All cactus seeds require a soil temperature of 21° to 27° C. (70° to 80° F.) for germination, and most of them germinate more surely and quickly in the range 27° to 33° C. (80° to 90° F.). Mature cacti are subject to damage from frost if the temperature falls below −10° to −5° C. (14° to 23° F.) for a short period or below −5° to −2° C. (23° to 28° F.) for a longer period. Under any given temperature range, turgid plants are much more susceptible to injury than plants with low water content. In spite of immunity to normal drought periods, cacti are abundant only in the regions in which the soil is periodically warm and moist at the same time, favoring both root absorption and germination, and in the regions in which winter minima are neither very low nor very prolonged. Small or procumbent species of cacti endure very cold winters in regions where the frost season is

preceded by a dry period, during which the water content of the plants is reduced.

The role played by succulents in the vegetation of the four deserts is sharply determined by the conditions which have just been outlined. Large columnar types (*Pachycereus Pringlei*, *P. pecten-aboriginum*, *Carnegiea gigantea*, *Lophocereus Schottii*, *Lemaireocereus Thurberi*) are all found in the warmer parts of the Sonoran Desert, and none of them beyond it except southward into the thorn forest. The arborescent cylindropuntias (*Opuntia fulgida*, *O. molesta*, *O. spinosior*, *O. cholla*, *O. Thurberi*, *O. echinocarpa*, *O. acanthocarpa*) are sparingly represented in the southern Mojave Desert by the last two, and in the Chihuahuan Desert by *O. imbricata* and *O. Kleiniae*. The platyopuntias are more sensitive to prolonged drought than any other type of cactus, and extensive stretches of the Sonoran Desert are almost devoid of them. The heaviest stands of these plants, *Opuntia discata*, *O. Engelmannii*, *O. phaeacantha*, *O. rhodantha*, *O. fuliginosa*, and others, are found at higher levels along the northern and eastern edge of the Sonoran Desert. They extend beyond the desert with little reduction in abundance into the desert-grassland transition, and are abundant in the Chihuahuan Desert. In the Mojave Desert the platyopuntias are represented almost solely by *O. basilaris*, a species which has little in common with the rest of the genus. In the Great Basin, as well as on the high plains of New Mexico, Colorado, and Nebraska, the platyopuntias are restricted in occurrence and represented by low species. Although they are the most widely distributed type of succulent, the platyopuntias do not range far beyond the Sonoran and Chihuahuan Deserts without great reduction in the number of species and in their prominence in the vegetation, as well as in the size of individual plants. The smaller types of cacti in the genera *Echinocereus*, *Mammillaria*, *Coryphantha*, and *Escobaria*, as well as the larger ones in *Ferocactus* and *Echinocactus*, are particularly important in the Chihuahuan Desert and well represented in the Sonoran Desert, but play a very unimportant part in the vegetation of the Mojave and Great Basin Deserts.

The two groups of herbaceous ephemeral plants found in the Sonoran Desert owe their existence not only to the biseasonal rainfall, but to the mild temperatures which permit growth at the time of the winter rains. In the Great Basin and the northern Chihuahuan Desert the cold winters confine activity of the ephemerals to the summer, whereas in the Mojave Desert the late winter is the only season in which their growth is possible.

Vegetational Features of the Sonoran Desert

A brief characterization of the Sonoran Desert was given in describing the four major subdivisions of the North American Desert. It is now proposed to treat in more detail the Sonoran Desert and its vegetational subdivisions. On account of the size of this area of nearly 120,000 sq. mi., it has been necessary to confine both the exploration and the descriptive text to the larger features of the plant covering. No precise statistical studies have been made, and no efforts to determine any of the sociological aspects of the smaller units of the vegetation.

Before taking up the regional treatment of the vegetation, it is desirable to

discuss some of the aspects of the plant life which are common to the entire area. Certain general features are exhibited by all deserts, but require discussion as exemplified in the Sonoran Desert. Also a description of the life forms is fundamental to a portrayal of the vegetation and its habital and regional differences.

General Features

HEIGHT. The average height of the dominant plants reaches its maximum in the arboreal desert of the foothills of Sonora. The largest individual trees, however, are found in the more open vegetation of the plains of central Sonora. The average height of *Acacia*, *Bursera*, *Lysiloma*, and *Prosopis* in the former region is from 5 to 6 m., but in the latter region the finest examples of *Cercidium*, *Olneya*, *Forchammeria*, and *Ipomoea* reach a height of 10 to 12 m. These dimensions are exceeded only by those of *Populus*, *Prosopis*, and other trees growing along streamways. A height of 11 m. is sometimes reached by *Carnegiea* and 16 to 18 m. by *Pachycereus* and *Idria*. Several yuccas exceed the normal height of the trees, notably *Yucca elata*, *Y. brevifolia*, and *Y. valida*. The plants which exceed a height of 6 m. rarely occur in such abundance that their collective tops seem to form the canopy of the vegetation. It is the trees which form the discontinuous canopy, above which tall cacti and yuccas project with great irregularity of height and spacing. Along the inner edge of the Vizcaíno Desert, in Baja California, *Yucca valida* is more abundant than the trees associated with it. At close range there seems to be great irregularity in its height, but in a longer vista its canopy has as regular a profile as does that of the pines of the southeastern United States, with a height of 7 to 8 m.

More than half of the Sonoran Desert is dominated by plants with a stature of less than 1.5 m. The extensive plains with nearly pure stands of *Larrea*, or with *Larrea* and *Franseria*, *Acacia*, *Lycium*, *Caesalpinia*, and numerous other plants, have a cover varying from 0.5 to 1.5 m. in height. It is only where nearly pure stands prevail or a single species is greatly in the majority that there is uniformity of height.

DENSITY. Openness of stand is almost a universal characteristic of the entire North American Desert. Many valleys in the Great Basin with favorable moisture and soil conditions bear nearly closed stands of *Atriplex confertifolia* or *Artemisia tridentata*. Restricted areas of *Larrea* and of *Acacia* with very little uncovered surface are occasionally seen in the Sonoran Desert. In far more than half of the Sonoran Desert, however, the plants cover less than 30 per cent of the ground area, and in at least one-fifth of it they cover less than 10 per cent of the surface.

These rough estimates for the entire region are based on a number of exact measurements in small areas. They have been made by regarding the plants as covering all of the surface that would be comprised if their tops were projected vertically onto the ground. Where several small shrubs grow under a tree, their areas are included in the coverage of the tree and do not contribute to the total. In their position as subordinates to the tree they do nothing to affect the open or closed appearance of the vegetation.

Greater density is commonly found in places where small shrubs are dominant than in the stands of larger shrubs or small trees. This is particularly true of areas in which *Franseria deltoidea* or *Encelia farinosa* forms a high percentage of the cover. It is also true of many overgrazed areas in southern Arizona which are now dominated by *Haplopappus Hartwegii*. It is not true of the region adjacent to the Colorado River in which *Franseria dumosa* is the dominant small shrub, as this region rarely shows more than a 15 per cent coverage.

Simplicity of composition. The number of species of large perennials composing the vegetation in the most unfavorable habitats is very small, and in the most favorable ones is not large. Simplicity of composition is found not only in the driest habitats, but also in situations where the soil is uniform in level, texture, and surface. This is true of the extensive nearly pure stands of *Larrea* in southwestern Arizona and northwestern Sonora, as well as of many smaller areas of *Atriplex* and *Lycium*.

The simplest composition is found on the low bajadas within 40 to 50 km. of the Colorado River and on the sandy plains of extreme northwestern Sonora, where 2 species, or sometimes 3, form the entire vegetation (*Larrea*, *Franseria dumosa*, *Hilaria rigida*). On plains and low bajadas below 300 m. elevation the total perennial flora has rarely been found to exceed 10 species in Arizona and 16 species in western Sonora.

With the prevailing simplicity of composition, it follows that the entrance or exit of a single species, or a great change in the relative abundance of two or more species, may make a profound change in the physiognomy of the vegetation.

Physiographic control of vegetation. So great is the importance to desert plants of the texture, depth, and surface character of the soil that in every area of adequate size there are differences in the vegetation which are closely correlated with these conditions. The same relations of vegetation to soil are presented over and over again in hundreds of valleys and intermont plains. There are hills or mountain slopes with rock in place and pockets of soil, there are pediments, upper bajadas with shallow, coarse soil, lower bajadas or plains with deeper soil of uniform but rather coarse texture, and flood plains or playas with deep, fine soil. The physiographic features of the basin determine the physical character and distribution of the soils, which in turn determine the vegetation.

It is impossible to institute comparisons between different parts of the Sonoran Desert without taking complete drainage basins into consideration, or at least the complete series of physiographic units and soil types found in each basin. In the moister regions on the east and northeast the distribution of vegetation is likewise controlled by the physiographic features, but in the driest parts of the Sonoran Desert and in the eastern Mojave Desert the relations are more weakly manifested. Here a low and open stand of *Larrea* and *Franseria* usually extends from the center of a basin, or the edge of its playa, to the summit of the surrounding hills.

CONSISTENCY OF LOCAL DISTRIBUTION. The trees, shrubs, and smaller perennials of the desert are unfailingly distributed over the areas which are favorable to them, no matter whether the stand is very open or relatively close. There is no suggestion of the mosaic type of distribution. Sporadic groups of the common perennials are rare except near the periphery of their geographic ranges. For a situation of given altitude, physiographic character, and slope exposure, the composition of the vegetation may be predicted with great certainty. It is only around springs and ponds or in relatively moist and shaded canyons that plants are to be found which are not of common occurrence. In this respect the desert with its small flora and simple vegetation forms a marked contrast with the moist temperate and tropical forests, in which scarcely any two hectares have the same flora.

The largest cacti (*Pachycereus*, *Carnegiea*, *Lemaireocereus*) and the solitary and caespitose ones (*Mammillaria*, *Coryphantha*, *Echinocereus*) are like the shrubs in the consistency and uniformity of their occurrence. Certain cylindropuntias which multiply almost solely by fallen joints (*Opuntia fulgida*, *O. cholla*, *O. Bigelovii*, *O. fulgida* var. *mammillata*) are conspicuously colonial in their occurrence. *Opuntia fulgida* and *O. cholla* owe some of their abundance to cattle, and the local dense colonies of these species are the product of favorable soil and the constant loosening of terminal joints by passing cattle. In ungrazed regions they are widely spaced, as are all the other cylindropuntias, in which the joints are not easily detached. *Opuntia Bigelovii* occurs only below 1000 m. and in the warmest situations, either on sandy soil or on the south slopes of hills. It is extremely abundant on certain hills and absent on adjacent ones of identical character. This distribution is apparently due to the increase of a small colony by vegetative multiplication and the inefficiency of dissemination by seed. The only plants showing inconsistent occurrence are these few cacti, which are the only plants of the area that exhibit vegetative multiplication.

SUBORDINATE PLANTS. In localities where there are trees and large shrubs it will be noticed that very many of them are closely surrounded by small perennials. The largest of these subordinate colonies are found under old trees with widespreading branches, where there is an accumulation of litter and dead annuals, and some humus in the soil. Close observation shows that a high percentage of the young individuals of the large perennials are in these situations and that many of the small perennials are more abundant there than elsewhere. It is significant that there are no subordinates under young and small perennials, which give little shade and have no accumulation of litter and humus; nor, for the same reason, are there any around *Carnegiea*, *Pachycereus*, *Lemaireocereus*, and *Lophocereus*.

The small perennials or semishrubs (*Encelia*, *Franseria*, *Viguiera*, and others) often shelter the early growth of their own seedlings as well as heavy stands of ephemerals. They do not commonly give shelter to the seedlings of large perennials. However, the period during which *Olneya*, *Bursera*, *Cercidium*, or *Pachy-*

cormus would be small enough to derive advantage from a location beneath the branches of *Encelia* or *Franseria* would commonly be much longer than the life of the last-named plants. This makes it difficult to estimate the number of young plants of *Olneya* or *Bursera* which apparently have sprung up in open spaces but really owe their start to the shelter of a semishrub which has long since disappeared.

The shade and proximity of either large or small perennials is a conspicuously favorable habitat for both winter and summer ephemerals (see pl. 30). The condition which is chiefly responsible is the slightly higher moisture content under the bushes and the longer duration of favorable moisture there. Fully as important as the amount of available water is the opportunity for interception and lodgment of wind-blown seeds. These move readily over the relatively smooth surface between bushes, but are caught by the bush itself and by the living or dead ephemerals already clustered about it. At the close of the growing season for ephemerals, the action of wind in disseminating seeds along the surface of the ground may be observed in any open situation, and it can then be seen that most of the crop comes to rest under large or small perennials or on very rough stony surfaces.

In many places in the driest parts of the Sonoran Desert subordinate plants are few under either large or small perennials. This is true of the sandy soils, on which the moisture conditions are much the same in the open and under trees or bushes, and on which the wind moves substratum as well as seeds (see pls. 5, 16, 34). It is also true of flat areas subject to overflow or deposition. Without small irregularities of surface and without the dead herbage of previous years, there is nothing to catch and hold wind-blown seeds on these smooth and level areas.

The colonies of seedling trees, small shrubs, grasses, and vines to be found under and around the large trees or oldest shrubs grow denser toward the central and southern part of Sonora, and include many species not found in the open. As the subordinate colonies increase in density, they also grow in extent and spread beyond the shade of the tree. On the inner half of the Sonoran plains between Hermosillo and the Yaqui River the stand of large perennials becomes denser than it is north or west of there, at the same time that the subordinate colonies spread more widely. As a result it is a common thing for several colonies to coalesce and, with the group of fostering trees, to form a sharply defined motte, or island, of vegetation. Broad expanses of bare or sparsely covered ground separate the mottes. It is obvious that many conditions are concerned in making the establishment of new individuals easier in the mottes or around their edges than in the intervening open areas.

Life Forms of the Sonoran Desert

The vegetation of the Sonoran Desert is distinguished from that of adjacent regions by the wide differences in appearance between its dominant plants. They are unlike in height, bulk, manner and amount of branching, character of stem, size, duration, color, and seasonal behavior of leaves, degree of succulence, and

time of flowering. The characteristic appearance of the landscape and the physiognomy of the vegetation are determined by the varied admixture and grouping of plants which exhibit these differences in structure and habit. Certain habitats are occupied by representatives of a large number of these types, particularly the hillsides, mountain slopes, and upper bajadas. The vegetation of plains and lower bajadas in the northwestern part of the Sonoran Desert is often reduced to three or four of the types. It is in the parts of the desert with 150 to 300 mm. (6 to 12 in.) of rain that the greatest number of types is found.

Investigation of representative members of nearly all the life forms of the Sonoran Desert was carried on at the Desert Laboratory for thirty-five years, and has thrown light on the ability of these plants to live in close association without serious disadvantage to any one of the types. In general there is no lack of room for the establishment of new individuals. In the rainy seasons the ground is often thickly covered with herbaceous ephemerals, among which there is competition for space and soil moisture. The seedlings of perennials must compete during their first season, and in some cases for several seasons, with the dense cover of ephemerals. The shoot growth of seedling perennials is outstripped by that of the ephemerals, but the roots of the young nonsucculent perennials penetrate as far as the roots of the ephemerals and in some species farther. The young perennial is therefore not seriously hampered in its first season by its short-lived associates so far as water supply is concerned, and indeed derives considerable advantage from the shade and shelter which they afford while they are alive and for many weeks after they die.

The successful establishment of a young perennial of any type depends upon whether its first few seasons are wetter or drier than normal and whether the particular spot in which it sprang up is sheltered or exposed, provided with deep or shallow soil, and protected or unprotected from a considerable change of surface level. The presence of closely adjacent mature perennials seems never to be an adverse circumstance in the fate of a young plant. On the contrary, the number of young plants that appear and survive close to mature ones greatly exceeds the number that appear and survive on the open or bare spaces.

These facts have an important bearing on the close association of diverse life forms in the vegetation of the Sonoran Desert. Establishment behavior is far from being identical in the various life forms, but no evidence has been found to indicate that any one of them has a more successful course of behavior than the others do; there are a few cases, however, in which individual species have acquired features of behavior which appear to be disadvantageous. In their germination and early growth the several life forms are under more nearly identical conditions than at any subsequent time. The development of their individual features of structure and behavior soon brings each form into a slightly different set of relations to the environment. Differences appear in height and spread of branches, depth and distribution of root system, and season of foliation and defoliation. These serve to separate the activities of some of the life forms, in either time or space, so as to reduce or eliminate the competition between them.

Table 2 (pp. 34–35) indicates the principal life forms of the Sonoran Desert and gives examples of them. Forms have been omitted which are of minor importance in the vegetation, as aquatics, vines, parasites, etc. The subdivision has been carried no farther than is necessary to illustrate the dissimilarity among the common plants of the region. Each of the examples given is a characteristic plant in some association in some part of the Sonoran Desert.

It seems desirable to discuss briefly the 25 life forms enumerated, in order to indicate their differences more clearly than is possible in the abbreviated key. Each of the forms is represented by a few or many clear-cut examples, in addition to which there are plants with intermediate characteristics which are not worthy of recognition as distinct forms in such a classification, but are of great interest as indicating the possible stages by which one life form may have been derived from another.

The EPHEMERALS (life forms nos. 1–3) constitute a large group, merging into the root perennials through a few common species of facultative perennials, the duration of which is controlled by rainfall fluctuations. The winter and summer ephemerals are distinct groups in the northern half of the Sonoran Desert, the time of their appearance being controlled by the prevailing range of surface soil temperature. Although related to one another in duration of life and in having a restricted season of activity, the ephemerals exhibit differences in habit, branching, stem, leaf, and other features which make them very unlike among themselves. For further discussion of these plants see chapter 4.

The ROOT PERENNIALS (4, 5), plants which persist from year to year strictly by underground organs, are all inactive in the dry seasons, and active either in winter or in summer, but in no case in both the moist seasons. There is no discoverable difference between the mechanisms for resting over the cool moist season, the warm moist season, and the dry ones, except that the few bulbous plants of the Sonoran Desert are active only in the cool moist season (*Allium Kunthii*, *A. haematochiton*, *Triteleiopsis Palmeri*, *Hesperocallis undulata*, *Calochortus Kennedyi*). Very large perennial roots characterize most of the Cucurbitaceae (*Cucurbita digitata*, *C. palmata*, *Brandegea Bigelovii*) as well as certain species in other families (*Rumex hymenosepalus*, *Phaseolus* spp.). In the cucurbitaceous genus *Maximowiczia*, part of the stem is enlarged into a turnip-shaped structure which is half buried and half exposed. The perennial organs in most of the members of this group are slender or moderately stout rhizomes; in some, they are the largest roots (*Delphinium*, *Anemone*). The root perennials are closely and perhaps genetically related to the semishrubs (17), in which the root system is perennial and the shoots commonly so but very sensitive to unfavorable moisture or temperature conditions.

Closely related in the manner of perennation are the GRASSES (6), in which the inner basal part of the cluster of shoots and leaves and the upper part of the root system persist under ordinary unfavorable conditions. Unlike the strictly underground perennials, the grasses show vegetative activity in both summer and winter, although flowering is confined to the former season.

Of great importance in the physiognomy of desert vegetation are the CAUDICAL

TABLE 2

LIFE FORMS OF THE SONORAN DESERT

Form	*Examples*
Ephemerals:	
Strictly seasonal:	
Winter ephemerals	1. Daucus pusillus, Plantago fastigiata
Summer ephemerals	2. Tidestromia lanuginosa, Pectis papposa
Facultative perennials	3. Verbesina encelioides, Baileya multiradiata
Perennials:	
Underground parts perennial:	
Perennial roots	4. Pentstemon Parryi, Anemone tuberosa
Perennial bulbs	5. Hesperocallis undulata, Brodiaea capitata
Shoot base and root crown perennial	6. Hilaria mutica, Aristida ternipes
Shoots perennial:	
Shoot reduced (a caudex):	
Caudex short, entirely leafy:	
Leaves succulent	7. Agave Palmeri, Dudleya arizonica
Leaves nonsucculent	8. Nolina microcarpa, Dasylirion Wheeleri
Caudex long, leafy at top:	
Leaves entire, linear, semisucculent	9. Yucca baccata, Yucca brevifolia
Leaves dissected, palmate, nonsucculent	10. Washingtonia filifera, Sabal uresana
Shoot elongated:	
Plant succulent (soft):	
Leafless, stem succulent:	
Shoot unbranched	11. Ferocactus Wislizenii, Echinomastus erectocentrus
Shoot branched:	
Shoot poorly branched:	
Plant erect and tall	12. Carnegiea gigantea, Pachycereus Pringlei
Plant erect and low or semiprocumbent and low	13. Pedilanthus macrocarpus, Mammillaria microsperma
Shoot richly branched:	
Stem segments cylindrical	14. Opuntia spinosior, Opuntia arbuscula
Stem segments flattened	15. Opuntia Engelmannii, Opuntia santa-rita
Leafy, stem not succulent	16. Talinum paniculatum, Sedum Wootoni
Plant nonsucculent (woody):	
Shoots without leaves, stems green	17. Holacantha Emoryi, Canotia Holacantha
Shoots with leaves:	
Low bushes, wood soft	18. Encelia farinosa, Franseria dumosa
Shrubs and trees, wood hard:	
Leaves perennial	19. Simmondsia chinensis, Larrea tridentata
Leaves deciduous:	
Leaves drought-deciduous:	
Stems specialized:	
Stems indurated on surface	20. Fouquieria splendens
Stems enlarged at base	21. Idria columnaris, Bursera microphylla

Form	*Examples*
Stems normal:	
Stems not green.....	22. Jatropha cardiophylla, Plumeria acutifolia
Stems green.....	23. Cercidium microphyllum, Parkinsonia aculeata
Leaves winter-deciduous:	
Leaves large.....	24. Populus Fremontii, Ipomoea arborescens
Leaves small.....	25. Olneya tesota, Acacia Greggii

PLANTS (7–10), a group of life forms characterized by a stout or somewhat succulent stem (caudex) in which the internodes are so greatly abbreviated that the leaves are inserted close to one another. Groups 7 to 9 are chiefly made up of members of the monocotyledonous families Bromeliaceae (*Hechtia*), Liliaceae (*Yucca*, *Nolina*, *Dasylirion*), and Amaryllidaceae (*Agave*). Group 7 includes, besides *Agave*, members of the Crassulaceae (*Dudleya*). *Agave* and *Dudleya* are very unlike in size and lignification, yet they are similar in having a short caudex completely covered by leaves, both caudex and leaves being succulent. Although the difference in size gives *Agave* and *Dudleya* distinct roles in the vegetation, nevertheless their similarity of relation to environment is indicated by the coincidence of the areas of maximum speciation and abundance for the two genera in western central Baja California.

The group of caudical plants in which the leaves are not succulent, but long and grasslike (8), is of some importance along the northern and eastern margin of the Sonoran Desert, and much more abundant just outside the desert. Only two genera (*Nolina*, *Dasylirion*) are represented. Far more abundant and characteristic in all parts of the Sonoran Desert is group 9, in which the leaves of mature plants are borne only at the top of the caudex and are either pliant and non-succulent or stiff and succulent. In the Sonoran Desert the group includes one arborescent *Dasylirion* and a number of species of *Yucca*. This essentially monocotyledonous life form is foreshadowed in the smaller mesic liliaceous plants *Xerophyllum* and *Tofieldia*. The characteristics of *Yucca* are intermediate between those of the dicotyledonous tree and those of the columnar cactus. The photosynthetic and transpiring surfaces are confined to the leaves, but are fixed in area so as to admit of no seasonal reduction. The trunk is from 10 to 75 cm. in diameter, and in *Yucca brevifolia* has a definite secondary thickening. The water content of trunk in all species and of leaf in the thick-leaved ones is great enough at the close of a rainy season to suggest the importance of these parts as storage organs, although they are without the mechanism which the Cactaceae have for adjustment to changes of volume.

The palms (10) are represented in the Sonoran Desert by members of only two genera with pinnately compound leaves and three with palmate leaf blades more or less dissected into linear segments toward their margins. The trunks of these trees are unbranched, often attaining a height of 20 m. or more with a diameter that rarely exceeds 1 m. The leaves remain attached to the trunk for a number of years if not removed artificially, or they may drop soon after they have ceased to

carry on photosynthesis. In *Washingtonia*, *Erythea*, and *Sabal* the persistent leaves form a dense thatch or "shag" that may hide a considerable portion of the trunk of healthy, unmolested trees; this situation is less pronounced in *Phoenix*.

The palms grow along watercourses, around seeps or potholes in rocky canyons, and on bajadas where the underground water supply is abundant. They rarely occur on dry hillsides or on plains more than one or two kilometers from the mouths of canyons. No special storage organs are present, but the spongy inner tissue of the trunks does hold a considerable amount of water and constitutes a reservoir from which moisture can be drawn for a limited time if the natural water supply is temporarily depleted. The leathery leaves are well adapted to reducing the loss of water by transpiration.

Owing to the rather specialized habitats necessary for the growth of the palms, they constitute a conspicuous element in the flora in only certain parts of the Sonoran Desert. *Erythea* is particularly abundant along the flanks of the southern part of the Sierra San Pedro Mártir in Baja California, and *Sabal* occurs in considerable numbers in the interior of Sonora. *Washingtonia* is less widely distributed and less abundant than either of the other genera just mentioned.

In the deserts of North America the STEM SUCCULENTS (11–15) are nearly confined to the Cactaceae, a family in which a wealth of types has developed. The only important stem succulent in the Sonoran Desert which is not of this family is *Pedilanthus*, if the halophyte *Allenrolfea* is left out of account as not being a strictly desert plant. The Cactaceae are of great importance in giving a characteristic physiognomy to the vegetation in nearly all parts of the Sonoran Desert. The life forms recognizable among the stem succulents may appear to be more distinctive in their mere geometry than in their essential relations to the environment. Study of the geographic and habital distribution of the five life forms has, however, given clear indication that their differences in size, form, and manner of branching are of fundamental importance in their sustained adjustment to different environments.

The barrel type of stem succulent (11) is found only in the genera *Ferocactus* and *Echinomastus* and is recognizable only by the lack of branching in a shoot which may be of any height from 1 dm. to 1.5 m. Injury to the single growing region of this type may stop further height growth or may in rare cases induce abnormal formation of several growing regions near the apex of the shoot. The barrel type is probably a derived rather than a primitive one, since it has few representatives in comparison with the similar branched types, and its simplicity of form is a development away from the prevailing condition in primitive cacti.

The columnar type (12) includes all the tallest and most massive stem succulents of the Sonoran Desert (*Pachycereus*, *Carnegiea*, *Lophocereus*, *Lemaireocereus*). Branching takes place either from mid height of the shoot or from the base. In sheer bulk these plants greatly exceed any others of the region, and there are only three nonriparian trees which reach greater height.

The small columnar type (13) resembles the barrel type, but its members are never more than 2 to 5 dm. high, with the exception of *Pedilanthus macrocarpus*.

This is the only euphorbiaceous plant in the Sonoran Desert which has strongly developed the succulent habit characteristic of so many of the family in the deserts of South Africa. The other members of this group are unbranched in early life and are then analogous to the plants of group 11. In later life they branch, usually from the base, and have from one or two to eight or ten erect or partly procumbent branches. A few forms branch so richly that the mature plant forms a compact hemisphere, superficially resembling alpine polster plants (*Echinocereus maritimus*, *Mammillaria fasciculata*).

The cylindropuntias (14) constitute a life form which is represented only by members of this section of *Opuntia*. The erect habit and frequent branching give the plants an arborescent form. The stems throughout are circular in cross section and segmented into joints, each of which is the outcome of a single season's growth. The tallest of this group are 2 to 3 m. in height (*O. fulgida*, *O. acanthocarpa*); others rarely exceed 1.5 m. (*O. Bigelovii*, *O. arbuscula*).

The platyopuntias (15) are also a life form restricted to the members of a section of *Opuntia*. The plant is either erect or prostrate and built entirely of flat joints of round, oval, or pyriform outline. In the tallest erect forms the oldest joints gradually assume a circular cross section and develop woody tissue of adequate strength for support (*O. chlorotica*, *O. laevis*). In the radiating branches of the prostrate forms the oldest joints often bear erect shoots of one to several joints (*O. rhodantha*, *O. phaeacantha*).

The life form in which succulent leaves are borne on a nonsucculent stem (16) is represented by a relatively small number of species which are only locally abundant. The leaves may be terete (*Portulaca lanceolata*, *Dudleya attenuata*) or broad and entire (*Talinum paniculatum*, *Nitrophila occidentalis*).

The NONSUCCULENT WOODY PERENNIALS (17–25) embrace the plants of greatest abundance in the make-up of the vegetation as well as the majority of the members of the flora.

The green-stemmed leafless plant (17) is represented in either ultimate, developmental, or incipient form by a large number of trees and shrubs. The ultimate form considered here includes a few trees and shrubs which are totally leafless after the seedling stage (*Canotia*, *Koeberlinia*, *Holacantha*, *Ephedra*). The multiphyletic origin of the leafless green-stemmed habit is obvious; initial stages of it are noted under 23 and may be seen in trees and shrubs which have evergreen leaves under usual conditions, as well as in deciduous shrubs which have well developed chlorenchyma immediately beneath a dark but translucent epidermis.

Among the nonsucculent leafy perennials of the Sonoran Desert are a large number of plants (18) characterized by soft wood, rich branching, indeterminate growth, and great responsiveness to favorable or unfavorable temperature or moisture conditions. The majority are from 5 to 8 dm. in height, but they may exceed 2 m. These will be alluded to as "semishrubs," in distinction from the true shrubs, which have hard wood, restricted branching, determinate growth, and marked ability to withstand cold or dry periods. The commonest semishrubs are *Franseria dumosa*, *F. deltoidea*, *F. magdalenae*, and *Encelia farinosa*,

four plants which vastly outnumber any others of any life form in the entire region. The semishrubs also include most of the perennial species in the genera *Atriplex*, *Eriogonum*, *Viguiera*, *Salvia*, *Haplopappus*, *Hyptis*, *Acamptopappus*, *Trixis*, *Franseria*, and many others.

The evergreen trees and true shrubs (19) include forms with thick, highly cuticularized leaves which are tenaciously held in long dry periods as well as through the winter (*Simmondsia chinensis*, *Jacquinia pungens*, *Atamisquea emarginata*, *Forchammeria Watsoni*, *Sapium biloculare*), forms with thinner and less xeric leaves which are shed in part during very dry periods (*Larrea tridentata*, *Condalia spathulata*, *Celtis pallida*, *Piscidia mollis*), and also forms with thin compound leaves which are retained throughout the year under favorable conditions, and after severe drought or cold die in place without a definite period of fall (*Olneya tesota*, *Coursetia glandulosa*, *Eysenhardtia orthocarpa*).

The perennials with definitely deciduous leaves (20–25) are divisible into those in which leaf fall is induced by drought, regardless of temperature conditions (20–23), and those in which defoliation occurs at the beginning of winter and new leaves appear in the spring more or less independently of the surface indications of soil-moisture conditions.

The small group of life forms in which the fall and appearance of leaves is most sensitive to fluctuating moisture (20) is also characterized by broad layers of tissue in the inner bark in which all cells are filled with resin. In the species of *Fouquieria*, which are the only examples of this growth form, the leaves are from 2 to 5 sq. cm. in area, thin, and mesic in every particular except the moderately heavy epidermis. When *Fouquieria* is in leaf, its water requirement is very high. When it is not in leaf, the armored stem is effectively protected from even a moderate water loss, and the requirement of the plant is very low. Under exceptional conditions the leaves may be retained for six months. The distribution of rainy periods is sometimes such that six or seven crops of leaves appear in one year.

Stout-stemmed drought-deciduous trees (21), herein designated as "sarcophytes," have few examples in the flora of the Sonoran Desert, but it happens that each of them is very abundant in its particular distributional area. In fact, the members of this group (*Idria columnaris*, *Bursera microphylla*, *B. filicifolia*, *Pachycormus discolor*, *Cyrtocarpa edulis*) and of the preceding form are second only to the stem succulents in giving the vegetation of the Sonoran Desert its characteristic physiognomy. *Idria* and *Pachycormus* are found almost solely in the region of winter rains and are in leaf only in that season. *Bursera* and *Cyrtocarpa* commonly come into leaf in summer as well as in winter. The exaggerated basal diameter of the stem of *Idria* is due to enlargement of the pith, and the surface is heavily indurated. In the other three trees the enlargement is confined to the cortex and periderm, and the smooth surface is not heavily armored. A slight basal enlargement of the trunk, either abrupt or tapering, is manifested by members of other life forms (22, 25), including other species of *Bursera* as well as *Jatropha*, *Ceiba*, and *Erythrina*.

A number of small trees have stems which are normal and large leaves which are drought-deciduous after the summer rainy season and do not appear at all in the winter rainy season. The group is related in behavior to the strictly winter-deciduous trees (24, 25), but is unlike them in producing its leaves at the beginning of the summer rains rather than at the advent of spring, and also unlike them in producing no leaves if the summer rains fail (*Jatropha cinerea*, *J. cuneata*, *J. cordata*, *Plumeria acutifolia*).

The important group of trees and shrubs (23) with green stems and small drought-deciduous leaves has been alluded to under 17 as constituting a stage in the development of the leafless green-stemmed form. In nearly all the members of this group the photosynthetic surface presented by the stems and twigs is greater than that seasonally provided by the leaves. The small-leaved forms produce foliage in summer and in winter (*Cercidium microphyllum*, *C. floridum*, *C. sonorae*, *Dalea spinosa*). Seasonal conditions sometimes enable the summer leaves to persist until the winter rainy season. The large-leaved forms produce foliage only in very favorable seasons and on the wood of that season (*Euphorbia colletioides*, *E. Xanti*, *Beloperone californica*). Many green-stemmed shrubs and semishrubs have small or linear leaves which persist throughout the year but are more numerous in the summer rainy season (*Krameria* spp., *Baccharis sarothroides*, *Porophyllum gracile*, *Bebbia juncea*, *Condalia lycioides*).

The winter-deciduous woody plants (24, 25) are characteristically represented by a group in which the leaves or leaflets are large (over 5 sq. cm.), the autumnal fall is rapid and complete, and the individuals are either confined to moist habitats (*Populus*, *Salix*, *Sapindus*) or else found only on the inner and more elevated edge of the desert (*Juglans*, *Fraxinus*). These are greatly outnumbered in species and individuals by forms of common occurrence in the desert, some of which have a leaf area as great as that of *Salix* or *Sapindus* (*Ipomoea arborescens*, *Ceiba acuminata*, *Tabebuia Palmeri*), but a larger number of which have compound leaves with small leaflets (*Prosopis juliflora* var. *velutina*, *P. juliflora* var. *Torreyana*, *Acacia Farnesiana*, *A. constricta*, *A. Greggii*). There is only a very broad line of separation between woody plants which are promptly and completely winter-deciduous and those that retain more than half their leaves through the winter, albeit in greatly impaired condition for performance of foliar functions. Several species of *Acacia*, *Mimosa*, and *Lysiloma* are more completely deciduous in northern Sonora than in the south. *Prosopis* is wholly deciduous in cold habitats, while at the same time near-by individuals in warmer situations retain many functional leaves. The behavior of all the plants of intermediate character is largely determined by the severity of the winter temperatures.

Vegetational Subdivisions of the Sonoran Desert

The attempt to subdivide the Sonoran Desert into areas which correspond to the natural botanical features of its several parts may be made from three standpoints: first, that of the geographic and physiographic groundwork which is so important in the diversification of the plant life; second, that of the genera

or species of plants which are most abundant in the various parts of the region; third, that of the character and organization of the communities of plants. From these three standpoints it is possible to make respectively geographic, floristic, and vegetational subdivisions. These are distinct in their rational basis even though their outlines happen to coincide to a greater or less extent.

It is obvious that the geographic subdivision relates largely to the environmental conditions, which are not a part of the plant life. Floristic and vegetational subdivisions must be made on the basis of their own intrinsic data. The physical setting is a controlling agent with reference to the vegetation, but is not one of its characteristics. The custom of using the habitat as part of the characterization of a plant community is an illogical procedure of long standing.

The designations for vegetational units or aggregates which are most acceptable in theory are unfortunately too cumbersome for repeated use. The adoption of established local names which owe their origin to the character of the vegetation, as marsh, chaparral, and tundra, has much to recommend it, but such a system would be very incomplete and would complicate the comparison of widely separated areas. In Latin American countries the terms used by the observant natives, as *cedral*, *sabinal*, and *corozal*, are simple and useful; yet these words, although they emphasize the dominance of a particular plant, tell nothing of the character of the community or of the principal associates of the dominant plant.

The subdivisions of the Sonoran Desert used in this publication have been made purely with reference to the vegetation. Names have been given to the subdivisions which refer solely—even if inadequately—to the character of the vegetation. Names have also been given these areas which indicate their preponderant or most distinctive genera. Finally, the areas have also been designated by names derived from their location or some outstanding geographical feature. In this way subdivisions have been given a vegetational basis at the same time that their floristic character has been indicated and brief geographical names have been provided for use in subsequent pages (see map 1).

The three sets of equivalent designations for the seven subdivisions are as follows:

1. Microphyllous desert
   Larrea-Franseria region
   Lower Colorado Valley
2. Crassicaulescent desert
   Cercidium-Opuntia region
   Arizona Upland
3. Arbosuffrutescent desert
   Olneya-Encelia region
   Plains of Sonora
4. Arborescent desert
   Acacia-Prosopis region
   Foothills of Sonora
5. Sarcocaulescent desert
   Bursera-Jatropha region
   Central Gulf Coast

6. Sarcophyllous desert
   Agave-Franseria region
   Vizcaíno Region
7. Arbocrassicaulescent desert
   Lysiloma-Machaerocereus region
   Magdalena Region

Brief Characterizations of Vegetational Subdivisions

1. Lower Colorado Valley. This is the largest subdivision of the Sonoran Desert, occupying the lower drainages of the Colorado and Gila Rivers, the Salton Basin, the extreme coast of Baja California as far south as Bahía Los Angeles, and all of Sonora lying below 400 m. elevation as far south as the valley of the Río Magdalena. The area is chiefly drained by the Colorado River and the Salton Sea, but its two southern extensions contribute their flood waters directly to the Gulf. The Lower Colorado Valley is well defined along its western edge and rather sharply marked between Parker and Phoenix as well as between Sonoyta and Santa Ana, but elsewhere is not sharply defined, since its typical vegetation occurs in restricted areas of valley floor in adjacent subdivisions.

In the Lower Colorado Valley the percentage of surface occupied by hills and mountains is less than in the other subdivisions. About 85 per cent of the area outside the delta of the Colorado is comprised in bajadas of low gradient, or in nearly level plains of gravelly outwash or sand. This subdivision is one of the most arid parts of the Sonoran Desert, being low in rainfall and soil moisture, and high in percentage of sunshine and in both summer and winter temperatures. The surface features are more diversified than in any of the other subdivisions, embracing volcanic and granitic mountains, sandy plains and dunes, alkali flats, and soils varying in origin, texture, and depth. The Lower Colorado Valley includes the delta of the Colorado River, where an abundant moisture supply gives rise to a series of vast hydric and mesic communities that have little in common with the surrounding desert vegetation. The history of the delta and its changes in historic time have been ably treated by Sykes (1926, 1937).

The vegetation of the Lower Colorado Valley is distinguished by its simplicity of composition on the gravelly and sandy plains which make up such a high percentage of the area. The upper bajadas, the level fields of recent volcanic eruptives, or malpais, and the hills and mountains support a richer vegetation. The two species which vastly outnumber all others are *Larrea tridentata* and *Franseria dumosa*, from which the designation Larrea-Franseria region is derived. Low, open stands in which these shrubs form from 90 to 95 per cent of the plant population cover thousands of hectares in all the larger intermont plains, and earn for the area its designation as microphyllous desert. On the rocky soil of upper bajadas and pediments are to be found small trees, notably *Prosopis juliflora* var. *Torreyana*, *Cercidium floridum*, *C. microphyllum*, and *Olneya tesota*. Larger individuals of the same trees are also to be found along the drainageways.

The poverty of the vegetation in perennial plants is compensated by a large flora of ephemeral herbaceous species. These have their most certain opportunity

and make their greatest display after the late winter rains, particularly on sandy soil west of longitude 114°. Summer ephemerals rarely appear in large numbers in that area, on account of the sporadic character of the summer rains there. On the eastern edge of the Lower Colorado Valley and in its southern extension in Sonora the summer ephemerals are abundant as well as those of the late winter.

The north-and-south extent of the Lower Colorado Valley is 650 km., a distance great enough to restrict some of the important dominants to the northern or the southern part of the area. There are also some notable floristic differences between the eastern and western edges of the area.

2. Arizona Upland. Under this designation is comprised the northeastern part of the Sonoran Desert, mainly in Arizona, partly in northern Sonora, and lying at elevations between 150 and 950 m. On the south and west the area merges into the plains of the Lower Colorado Valley; on the north and east it is flanked by a broken series of mountains, most of which rise above the level of desert conditions and vegetation. The limit of the vegetation of the Sonoran Desert is here clearly marked, although a few of its characteristic plants occur as high as 2000 m. in the mountains.

The principal part of the Arizona Upland drains, actually or potentially, into the Gila River. A small area at the north is drained by the Bill Williams River, a very small part in the southwest by the Sonoyta, and the southernmost extension by the Altar, Magdalena, and San Miguel Rivers. Throughout this area the landscape is studded with small mountains and hills, which cover a much greater percentage of the total surface than in the Lower Colorado Valley. Only along the lower courses of the Santa Cruz and Gila Rivers and southeast of Sonoyta are there extensive valleys, and it is in them that the vegetation of this area most closely approaches that of the Lower Colorado Valley. The rainfall ranges from about 75 to 300 mm. and is biseasonal throughout the area.

The vegetation of the Arizona Upland exceeds that of the Lower Colorado Valley in stature, density, and the number of species which play a dominant or subdominant role. *Larrea* is still an important plant in nearly all situations, but has a greater number of associates. *Cercidium microphyllum*, though absent from the lower bajadas, is elsewhere so abundant as to characterize the area. Other important species are *Prosopis juliflora* var. *velutina*, *Olneya tesota*, and *Fouquieria splendens*. The cacti are numerous and diversified, the most conspicuous ones being *Carnegiea gigantea*, *Ferocactus Wislizenii*, and 12 or 15 species of cylindropuntia and platyopuntia. A considerable number of large and small shrubs occur here and do much to add to the density of the ground cover. Perennial grasses are locally abundant. Both winter and summer ephemerals carpet the ground in favorable seasons. As contrasted with the Lower Colorado Valley, there are fewer species of the former group and more of the latter.

From the floristic viewpoint the Arizona Upland may well be designated the Cercidium-Opuntia region, as these two genera play a more important part in its vegetation than do any others (except *Larrea*) and are more important here

than in any other subdivision of the Sonoran Desert. It is from the important role of the succulents, including *Carnegiea*, that the Arizona Upland is called crassicaulescent, or stem-succulent, desert.

3. Plains of Sonora. Lying between the foothills and the coastal strip in central Sonora is an area which has some physical features in common with the Lower Colorado Valley. The general surface is very regular, with an inclination from 750 m. elevation on the inner edge to 100 m. on the outer. The mountains and hills are few and do not exceed 10 per cent of the total area. Only four mountains rise above 1000 m. The surface is coarse or fine gravelly outwash, with only small accumulations of sand marking the terminus of clogged arroyos. Although some of the mountains are volcanic, there are no recent malpais fields. The rainfall is 250 to 375 mm., an amount substantially greater than in the Lower Colorado Valley. Frost is less frequent and less severe than in the areas to the north. Summer temperatures are more moderate than those in the Lower Colorado Valley.

The vegetation of the Plains of Sonora is dominated by trees and shrubs, because of which it is designated arbosuffrutescent desert. The name Olneya-Encelia region is suggested by the dominant tree and shrub. The trees are remarkable for the size which they attain under desert conditions, and also for their abundance on the inner half of the area. *Olneya tesota*, *Cercidium microphyllum*, and *Prosopis juliflora* var. *velutina* are the dominant species. In this area *Larrea* reaches the southern limit of its importance, occurring only locally in the most favorable situations. The dominant shrub is *Encelia farinosa*, which is confined to rocky slopes in the two subdivisions to the north. In this area *Cercidium sonorae* and *Fouquieria Macdougalii* reach their northern limit and are locally abundant. Conspicuous elements of the vegetation are the large columnar cacti *Lemaireocereus Thurberi* and *Lophocereus Schottii*. *Carnegiea* is here greatly reduced in abundance. The only other important representatives of the cacti are four species of *Opuntia* (*O. Thurberi*, *O. arbuscula*, *O. fulgida*, and *O. leptocaulis*) and the tall but slender *Rathbunia alamosensis*. A large number of shrubs and semishrubs are abundant on the Plains of Sonora, growing in the stands of *Encelia* or *Larrea*, in the protection of the larger trees, or on the hills and lower mountain slopes. Many of these also occur in the Arizona Upland, but a high percentage reach their northern limits here or in the Sonoran part of the Central Gulf Coast. Along the banks of the larger and smaller arroyos of the Plains of Sonora the trees and shrubbery are often thickly massed and in strong contrast with the open vegetation between the drainageways. These thickets provide shade and slight betterment of moisture conditions which favor the occurrence of many vines, root perennials, and small shrubs not found in other habitats.

4. Foothills of Sonora. The easternmost subdivision of the Sonoran Desert extends from the vicinity of Arizpe, on the Río Sonora, southward to the delta of the Río Yaqui, falling gradually from about 1000 m. to sea level. On the west it

passes with remarkable sharpness into the Plains of Sonora, on the north it follows up the valleys of Río Sonora, Río Moctezuma, and Río Bavispe, on the east it extends to the oak grassland of the lower mountain slopes, and south of 28° N. it merges gradually into thorn forest. Except at its southern end the entire area is rolling or hilly, with only narrow stretches of plain at intervals along the larger rivers. The mineralogical material is chiefly older volcanics or limestone, but there are large lava fields in the Moctezuma Valley and between Río Moctezuma and Río Sonora which appear to be of relatively recent origin. The delta of the Río Yaqui is a featureless alluvial plain over 50 km. in diameter. Part of it is devoted to the cultivation of rice, but much of it is in a natural or nearly natural condition.

The Foothills of Sonora constitute the least desert part of the Sonoran Desert. Incomplete records indicate that the rainfall near the center of the area has, at least in certain years, been slightly more than 500 mm. Whereas summer and winter rains are nearly equal in the Arizona Upland, there is a higher percentage of summer rain in the Foothills of Sonora. The time and duration of the rainfall seasons are not greatly different in the two subdivisions. In spite of the heavy summer rainfall, the Foothills area is subjected to long drought periods, and these are accentuated in their effects on the vegetation by the fact that the warm season is longer in the Foothills and that the drought periods are accompanied by slightly higher temperatures.

The most noticeable features of the vegetation of the Foothills of Sonora are the abundance of small trees (from which it is called arborescent desert), the frequent mottes of dense shrubbery, the amount of grass at higher elevations, the infrequency of cacti, the occurrence of palms, and the appearance among the dominant perennials of many trees and shrubs not found elsewhere in the Sonoran Desert.

Comparable situations in the northern and southern parts of the Foothills differ in their physiognomy and dominant woody plants. Toward the south a number of trees are important which reach their northern limits in the Foothills subdivision. Toward the north the upland vegetation is more open, with a greater amount of grass. On the flood plains and well watered level areas *Prosopis juliflora* var. *velutina* is the dominant tree in the north, but in the south it shares its dominance with *Acacia cymbispina* and *Lysiloma divaricata*, giving rise to the designation Acacia-Prosopis region. Throughout the upper half of the area the secondary trees and the shrubs along the arroyos are chiefly the same that are characteristic of the Arizona Upland. On rocky slopes and coarse outwash at all but the highest elevations of the Foothills, the stand of trees and shrubs is heavier than in any but the most favorable situations in the Arizona Upland. With few exceptions the trees have small leaves or leaflets which are wholly or almost wholly deciduous. The trees of commonest occurrence are *Bursera odorata*, *Jatropha cordata*, *Cercidium sonorae*, *Olneya tesota*, *Fouquieria Macdougalii*, *Bursera laxiflora*, *Guaiacum Coulteri*, and *Ceiba acuminata*. Shrubbery plays an important role in giving a more closed appearance to the vegetation, the principal species being

Caesalpinia pumila, *Dodonaea viscosa* var. *angustifolia*, *Haematoxylon brasiletto*, *Celtis pallida*, *Karwinskia Humboldtiana*, *Franseria cordifolia*, and *Randia Thurberi*.

The general aspect of the vegetation is more monotonous in the Foothills of Sonora than in the Arizona Upland. Large cacti, yuccas, and agaves are less frequent in the Foothills and not so conspicuous as in more open vegetation. In the southern part, *Pachycereus pecten-aboriginum* is a common associate of acacias and other trees. In many places the palm *Erythea Roezlii* occurs in groups along arroyos or scattered singly over the rolling valleys. The arborescent *Nolina matapensis* is common in scattered colonies.

There is a heavy growth of herbaceous plants in almost all situations during the summer, but the number of species involved in the display is not so great as in the Arizona Upland. There are a few herbaceous plants which are active only in the late winter. The herbaceous root perennials outnumber both groups of ephemerals and are of greater importance in the vegetation of wholly undisturbed situations.

5. Central Gulf Coast. The close similarity of the vegetation on the two sides of the head of the Gulf of California is not maintained in the central part of the Gulf. The vegetation of the opposed shores is, however, very closely related, as well as very distinct in each case from that of the interior. The Central Gulf Coast subdivision embraces the Sonoran coast from the mouth of Río Magdalena nearly to the mouth of Río Yaqui, and in Baja California extends from Isla Angel de la Guarda in a thin and broken strip to San José del Cabo. Throughout the two parts of this area the vegetation is almost identical in physiognomy, and a large number of its component species are the same. There is, however, a floristic difference between the parts such as is only feebly manifested nearer the head of the Gulf.

The rainfall of the Central Gulf Coast is very low and uncertain. The summer temperatures are very high, except when those of the immediate shore are ameliorated by onshore winds. The hills are bare of soil, and the streamways are bordered by aprons of sand and boulders. In the few places where there is an underground seepage of water, the vegetation forms a sharp contrast with that of the surroundings. The activity of the plants is determined by the occurrence of rain, and is sporadic rather than seasonal. Rain may fall either in the latter half of the winter or in midsummer, but is frequently lacking, sometimes for several seasons in succession.

Among the plants which are abundant in the Central Gulf Coast subdivision are the sarcocaulescent trees, with trunks of exaggerated diameter, including *Bursera microphylla*, *B. Hindsiana*, *Jatropha cinerea*, and *Idria columnaris*. This has therefore been designated the sarcocaulescent desert, or Bursera-Jatropha region. Although these striking trees are, in their abundance, distinctive of the area, they are actually outnumbered by *Olneya tesota*, *Cercidium floridum*, *Fouquieria splendens*, and *Prosopis juliflora* var. *Torreyana*, and by small-leaved shrubs, the identity of which is often determinable only in a favorable season.

The only evergreen shrubs are *Larrea tridentata*, *Viscainoa geniculata*, *Maytenus phyllanthoides*, and *Stegnosperma halimifolium*. The most abundant deciduous shrubs are *Jatropha cuneata*, *Encelia farinosa*, *Lycium Andersonii*, *Euphorbia misera*, and *Solanum Hindsianum*, accompanied by small, shrublike individuals of the trees that have been mentioned. Succulent plants are represented locally but are often lacking over large areas. *Pachycereus Pringlei*, like *Idria columnaris*, is much more local than in the interior of Baja California, and the most common cacti are the cylindropuntias, including *Opuntia Bigelovii*, *O. cholla*, *O. ramosissima*, *O. tesajo*, and *O. clavellina*.

The banks of washes and sandy flood plains have the heaviest vegetation in the Central Gulf Coast subdivision and the largest trees of *Cercidium floridum*, *Prosopis juliflora* var. *Torreyana*, *Bursera Hindsiana*, *Olneya tesota*, and *Dalea spinosa*. All the shrubs mentioned reach greater size and abundance along drainageways. Dense thickets often occur which are made up of very large individuals of *Hymenoclea pentalepis*, *Bebbia juncea* var. *aspera*, *Hyptis Emoryi*, and *Lycium brevipes*, accompanied by a number of other shrubs and a few vines. After heavy rains, ephemeral plants are abundant on sandy soil, but are few on the coarse soils and hillsides.

6. Vizcaíno Region. The central third of the Pacific coast of Baja California presents conditions and plant life very unlike those of the corresponding coast of Sonora. The Vizcaíno Region of the Sonoran Desert extends from the vicinity of Rosario to Punta Pequeña, west of Comondú, and runs inland approximately to the drainage divide of the peninsula, except at the extreme south. This area differs from the desert-chaparral transition region, lying between San Diego and Rosario, in the greater distance to a mountain background. For that reason the maritime influences scarcely extend more than 10 km. inland in any part of the Vizcaíno Region. A light winter rainfall occurs, which is more certain in the north than in the south and is extremely uncertain in much of the interior. Summer storms visit the mountains and hills along the eastern edge of the area on rare occasions. The immediate coast has the poorest vegetation of any part of the area, and no distinctive plants except those of the strand itself. Shrubs, cacti, and stones are heavily covered with lichens, and the epiphytic *Tillandsia recurvata* is very abundant. Although the humidity of the ocean wind is usually between 50 and 60 per cent, it does little to contribute moisture to the soil, and its average velocity is high enough to make it an important factor in transpiration. The strong and almost constant wind is apparently chiefly responsible for the very open and stunted vegetation of the coastal strip.

The Vizcaíno Region presents a hilly or rolling surface with a few small mountain areas and many rough fields of volcanic rock. A coastal plain over 50 km. in length and width has developed at the head of Vizcaíno Bay and extends southeastward toward San Ignacio. It is bounded on the southwest by the rugged Sierra Vizcaíno, and widens into another triangular area around the Laguna de San Ignacio. Outside this area, known as the Vizcaíno Desert, the only level

ground with deep soil in this subdivision is to be found in a few very small valleys near the coast. The principal soils are the scanty pockets found on stony slopes, a very fine red volcanic clay, the alkaline clay of the outer Vizcaíno Desert, and the areas of sand along the coast, which appear to have been derived from the beach. The most favorable soils of the area are the coarse outwash of the inner Vizcaíno Desert and the volcanic clay.

The distinctive feature of the vegetation of the Vizcaíno Region is the rich development there of the sarcophyllous or leaf-succulent plants, which play only a minor role in the vegetation of other parts of the Sonoran Desert. The most conspicuous ones are several large species of *Agave*, but the smaller Dudleyas are even more abundant, being numerous in many habitats where *Agave* is uncommon. The most nearly omnipresent of the shrubby perennials is *Franseria chenopodifolia*, which gives a light-gray tone to the landscape in all but the most rocky situations. The sarcophyllous desert may well be designated floristically as the Agave-Franseria region. Almost as important as *Agave* in this area is the giant *Yucca valida*, which grows in great abundance in all areas with deep soil, but is absent from a very considerable part of the interior. The range of *Idria columnaris* coincides closely with the Vizcaíno Region; this species is very abundant on fine and coarse outwash soils, but is absent from the Vizcaíno Desert and the inner hills. The sarcocaulescent *Pachycormus discolor* is also nearly confined to this subdivision, exhibiting its most grotesque forms on rocky slopes near the sea but attaining its greatest height and abundance on gentle slopes in the interior.

The well deserved reputation for uniqueness enjoyed by the vegetation of Baja California is chiefly based on the occurrence of *Idria columnaris*, *Pachycormus discolor*, *Fouquieria peninsularis*, *Pachycereus Pringlei*, *Yucca valida*, *Agave Shawii*, *Viscainoa geniculata*, and *Glaucothea armata* in the optimum habitats of the Vizcaíno Region. It is of interest that all these dominants are confined to this area and the one immediately to the south, except for a few known localities for four of them in Sonora. In spite of the abundance of this galaxy of striking plants in the best situations, in far more than half of the Vizcaíno Region they are all rare or absent. It is distinctly an area of barren slopes and alkaline or extremely arid valleys with a low stand of *Franseria chenopodifolia*, *F. magdalenae*, *Atriplex polycarpa*, *Larrea tridentata*, *Lycium californicum*, *Machaerocereus gummosus*, *Viguiera deltoidea*, and *Lycium Fremontii*. The areas of salitral, or alkaline plain, in the southern part of the Vizcaíno Desert are extremely poor in plants, and some of the plateaus and rolling plains above 500 m. are thinly covered by a simple stand of *Atriplex polycarpa* and *Lycium californicum*. The contrast between the areas of richest and poorest vegetation is greater here than in any other subdivision of the Sonoran Desert.

7. Magdalena Region. This area embraces the desert of the southern third of the peninsula and lies entirely in the Pacific drainage. It extends from the vicinity of San Ignacio nearly to Todos Santos, and throughout its southern half desert interdigitates with the arid type of low forest characteristic of the

Cape Region. North of Comondú the drainage divide of the peninsula and the eastern edge of the Magdalena Region are formed by the Sierra de Santa Lucía, Sierra de las Palmas, and Sierra de Zacatecas. These small mountains have been the centers of vigorous volcanic activity, giving origin to extensive malpais fields which cover the northern part of this subdivision from the mountains nearly to the sea. South of Comondú the eastern boundary of the area lies along the lower slopes of the Sierra de la Giganta, 10 to 20 km. west of the drainage divide. These slopes drain into the Magdalena Plain, which occupies nearly the width of the peninsula between latitude 24° and 26° N. The coast is bordered by lagoons and sand dunes. The interior of the plain has fine or moderately coarse alluvial soil with innumerable playas ranging from several hundred hectares to a few square meters in area. A few of the largest streams draining the Sierra de la Giganta flow through seasonally to the Pacific, but a very large proportion of the drainage is indeterminate or spills from one playa to another. The coastal half of the plain is very poor in small drainageways. At the close of a rainy period the plain abounds in lakes and in meadows which have been formed by the silting of old playas and the invasion of palustrine plants.

The marked difference between the soil conditions of the malpais mesas in the north and the Magdalena Plain in the south results in types of vegetation which differ greatly in physiognomy, stature, and the local allocation of individuals. There is also some difference in the groups of species characteristic of the two soil regions, and a great difference in their relative abundance. With respect to the entire flora there is a very strong floristic difference between the Magdalena and Vizcaíno Regions. In the lists of dominant species which give character to the vegetation the difference is much less. The absence of *Idria columnaris* and the relative scarcity of *Pachycormus discolor*, *Yucca valida*, and *Agave Shawii* in the Magdalena Region does much to distinguish the two areas. The physiognomy of the vegetation in the Magdalena Region is distinctly that of the desert. If the vegetation is viewed only with reference to the habit and form of the plants and the organization of the communities, it strongly resembles that of the hills and plains of central Sonora. As a whole the area exhibits an abundance of large cacti, notably *Pachycereus Pringlei*, *Machaerocereus gummosus*, *Lemaireocereus Thurberi*, and *Opuntia cholla*, together with a frequency of small trees in all situations except malpais, including *Prosopis juliflora* var. *Torreyana*, *Lysiloma candida*, *Cercidium peninsulare*, *Bursera laxiflora*, *Fouquieria peninsularis*, and *Jatropha cinerea*. The most distinctive feature of the Magdalena Region division is the equality of dominance between trees and large succulents, and it is accordingly designated arbocrassicaulescent, or tree and stem-succulent, desert. The examples of these two types of plant which are most abundant in the area are *Prosopis juliflora* var. *Torreyana* and *Pachycereus Pringlei*, but it seems best to derive the floristic designation from two examples which are almost as common and more distinctly characteristic of the area. These are *Lysiloma candida* and *Machaerocereus gummosus*, from which this is styled the Lysiloma-Machaerocereus region.

Lower Colorado Valley

(Microphyllous Desert. Larrea-Franseria Region)

The strongest impressions given by the vegetation of the Lower Colorado Valley are of uniformity over wide areas, and simplicity of composition. These impressions are strengthened by the fact that they are particularly true of the plains and bajadas which form such a high percentage of the entire surface. Closer examination of the area reveals the importance of the substratum in determining the stature, density, and composition of the vegetation. Though this is true of all parts of the Sonoran Desert, and indeed of almost all vegetational areas, it is less manifest in the two most arid subdivisions (the Central Gulf Coast and the Lower Colorado Valley) than it is in the others. Wide differences exist between the vegetation of rocky slopes and that of gravelly plains, and between that of volcanic and of granitic hills, but there is often a close vegetational similarity between the gravelly and sandy plains. *Larrea* and *Franseria* retain their dominance on a series of soils which differ greatly in depth and texture, and they are also constituents of the vegetation on malpais and volcanic hills. These two plants are either dominant or abundant under differences of substratum which would support dissimilar vegetation under more favorable moisture conditions. This is due to the remarkable physiological constitution of these shrubs, and also to the simplicity of the flora, which has given them little competition. The simplicity of the flora, as a fact in itself, means merely that no other shrubs have developed biological and physiological characteristics so highly suited to survival in this region as are those of *Larrea* and *Franseria*.

INTERMONT PLAINS AND BAJADAS. These features form a great network throughout the Lower Colorado Valley, with mountains and hills filling the irregular meshes. The plains are commonly separated from the mountains by pediments and bajadas of varying width, but this condition is not invariable. Many hills and some of the small mountains are built of such durable rock that they have yielded almost no outwash material under the prevailing low rainfall, and in such cases the intermont plains extend to the base of the mountain slope. The width and gradient of the zone of pediment and bajada which surrounds most of the mountains is determined by the size of the mountain and the readiness with which its material is eroded. The recent eruptives are very resistant and supply little or no material for the formation of a bajada. Older volcanics and granitic rocks weather more readily and give rise to bajadas which may be short and steep, as in the Californian parts of the area, or long and of low gradient, as is common in Arizona and Sonora. The line separating bajada from intermont plain is never clear-cut, except where the base of a very steep bajada has been accentuated by the development of a drainageway paralleling the base. Under usual conditions the lower part of the bajada merges very gradually into the intermont plain, with only slight change in gradient. In the largest plains there is a fall of 4 to 9 m. to the kilometer.

The nearly pure stands of *Larrea* and *Franseria* which dominate all the intermont plains and lower bajadas in the Lower Colorado Valley are usually very uniform throughout a given plain. The number and spacing of the plants is nearly the same from hectare to hectare, their relative numbers are nearly the same, and their height is uniform. When widely separated plains are compared, considerable difference is often found in the structure of this simple community. Where the rainfall is 100 mm. or less, the stand of plants is very open, as on many of the lower bajadas north of the Chocolate Mountains in California and throughout the extension of the area into Baja California. Along the northeastern edge of the area the stand of *Larrea* is much heavier and the plants are taller, as in McMullen Valley and the Harquahala and Palomas Plains, in Arizona. In general the spacing of individuals is more uniform for *Larrea* than for *Franseria*, and there seems to be no complementary relation between the abundances of the two plants. *Franseria* is most abundant on plains with sandy loam to a depth of at least 1 m. (see pl. 11), and its numbers are much reduced on gravelly bajadas, although the plants found there are large. On the deep clay loam plains of Sonora, south of Río Magdalena, *Franseria* is far less abundant than elsewhere in this area. The plant coverage in the microphyllous desert usually ranges from 3 to 12 per cent.

On the plains and lower bajadas *Larrea* and *Franseria dumosa* form from 90 to 100 per cent of the vegetation. The remaining small percentage is made up of shrubs and cacti, some of which are commoner in other situations. Small trees or shrubs of *Prosopis juliflora* var. *velutina* and *Cercidium floridum* are rare, *Fouquieria splendens* is infrequent and indicates a spot with thin or stony soil, *Atriplex canescens* is infrequent, and *Hilaria rigida* is frequent in parts of Yuma County, Arizona. In the following list of plants characteristic of the plains and lower bajadas, the habitats in which they are more abundant are indicated.

Plants of intermont plains and lower bajadas in the Lower Colorado Valley

Larrea tridentata	
Franseria dumosa	
Opuntia ramosissima	
Opuntia echinocarpa	Upper bajadas
Lycium Andersonii	Margins of washes
Condalia lycioides	Margins of washes
Franseria deltoidea	Upper bajadas
Hilaria rigida	Sandy plains
Krameria Grayi	Upper bajadas, hills
Prosopis juliflora var. velutina	Margins of washes, flood plains
Cercidium floridum	Margins of washes, upper bajadas
Echinocereus Engelmannii	Upper bajadas
Encelia frutescens	Margins of washes
Atriplex canescens	Alkaline flats
Hymenoclea monogyra	Margins of washes, sandy arroyos
Opuntia Wrightiana	
Fouquieria splendens	Upper bajadas, hills

All evidence as to the physical conditions indicates that the intermont plains and lower bajadas of the Lower Colorado Valley are one of the most unfavorable habitats of the Sonoran Desert from the standpoint of water relations. These conditions are met by the dominance of two perennials and the infrequent occurrence of 15 other species, all but two of which are more abundant in other habitats. The two exceptions, *Opuntia ramosissima* and *O. Wrightiana*, are found elsewhere only on the sandy plains, where they are rare. These two cacti and *Hilaria rigida* are the only plants mentioned above which do not occur in any of the more favorable habitats of the Sonoran Desert, as do even the two dominant shrubs.

The importance of a very slight betterment of the moisture conditions is shown by the vegetation along the margins of very small drainageways. Water flows in these outlets from four or five to twelve or fifteen times each year, to judge from the average number of rains producing runoff. The conditions for penetration of water are better than on the neighboring surfaces, and the sand which commonly forms the bed of the drainageway serves to retard surface evaporation. These circumstances increase the moisture of the soil during the growing periods and also slightly prolong the periods. During much of the year the conditions are not better than elsewhere. Plants are more abundant along the drainageways and reach greater size; also, species occur there which are absent from the level surfaces. The response of the vegetation to the slight and temporary betterment of water supply merely serves to emphasize the adverse conditions to which the plants of the level ground are subjected. In large drainageways the volume of water carried after rainstorms is greater and the bed of sand is thicker. A considerable percentage of the runoff is therefore stored under and along the arroyos, and large trees of *Prosopis*, *Cercidium*, and *Dalea* are found in close proximity to open stands of *Larrea* and *Franseria*.

Not only the size of drainageways, but also the character of their distribution over the land surface is important to the vegetation. Two types of lesser drainage pattern are found in the Lower Colorado Valley. One is the dendritic type, of general occurrence elsewhere, in which the flood waters are gathered into larger and larger streamways and the drainage assumes a definite course. The other is the reticulate type, in which the drainageways anastomose, increasing little in size as they progress down slope, and forming a continuous network of shallow rills which fail to contribute to the formation of a through drainage system. Dendritic drainage develops under heavier rainfall and in regions of greater relief. Reticulate drainage is found under very low rainfall, where the detrital load of the storm water is heavy, and where the goal of the flood water is a playa or a plain rather than a large streamway originating at a distance.

The reticulate type of drainage is common to nearly all of the Californian part of the Lower Colorado Valley and to approximately half of the remainder of the area. Between Yuma and Niland the main line of the Southern Pacific Railroad runs at right angles to the general direction of the reticulate drainage from the Chocolate Mountains. After a torrential rain the flood water is a menace

to the railroad embankment, and its disperse distribution has been controlled by placing culverts at regular intervals and connecting them by A-shaped dikes running about 200 m. up the slope.

Where the drainage is dendritic, the slightly heavier vegetation along the drainageways follows them closely and makes a treelike pattern when the plain or bajada is viewed from an elevated spot. Where the drainage is reticulate, the plants of slightly higher water requirement do not form continuous belts along the shallow washes, but nevertheless are often so abundant that they appear to be part of a uniform community covering the entire bajada. The species of plants favored by the two types of drainageway are the same, but their allocation is so different that it affects the physiognomy of the vegetation.

The trees which are most abundant along large drainageways are *Prosopis juliflora* var. *velutina* or *P. juliflora* var. *Torreyana*, *Cercidium floridum*, *Olneya tesota*, and *Dalea spinosa*. The height and size of the trees is roughly proportional to the size of the drainageway. Along the smallest washes they may occur as mere shrubs or may be absent. The commonest plants along the small drainageways are *Hymenoclea monogyra* or *H. pentalepis*, *Baccharis sarothroides*, *Lycium Andersonii*, and *Acacia Greggii*. The following list of plants characteristic of the margins of drainageways covers the plains and lower bajadas of the entire Lower Colorado Valley. Those found only in the northern or southern parts of the area are indicated. The species commonest in sandy washes are also indicated.

Plants of margins of drainageways in intermont plains and lower bajadas in the Lower Colorado Valley

Prosopis juliflora var. velutina
Prosopis juliflora var. Torreyana
Cercidium floridum
Olneya tesota
Dalea spinosa (sand)
Baccharis sarothroides
Hymenoclea monogyra (sand)
Hymenoclea pentalepis (southern; sand)
Lycium Andersonii
Acacia Greggii (northern)
Condalia lycioides
Chilopsis linearis
Franseria ambrosioides
Larrea tridentata
Encelia frutescens
Beloperone californica
Anisacanthus Thurberi
Sapium biloculare (southern)
Celtis pallida (northern)
Horsfordia alata (southern)
Franseria cordata (southern)
Phaulothamnus spinescens (southern)
Berginia virgata (southern)
Acalypha californica (southern)
Stegnosperma halimifolium (southern)
Bebbia juncea var. aspera (sand)
Solanum Hindsianum (southern)

In previous discussion of physiographic features (p. 49) mention has been made of the gradual change in the texture, depth, and surface of the soil on nearly all bajadas when they are followed from top to base. Large mountains of great age are surrounded by a zone of pediment, on which the soil is coarse and thin, or in rare cases is confined to pockets in a planed surface of rock in place. There is great variation in the distance to which pediment extends from the base of a

mountain and in the depth of the outwash and soil by which it is covered. Throughout the Sonoran Desert, upland vegetation is strongly influenced by the character of the substratum to a depth of 1 m., but it is not influenced by differences in the nature of the soil below 2 m. The plant cover differs as between planed rock surface, shallow soil with a partially weathered rock base, and deeper soil with many included boulders, but no differences can be detected between spots in which the pediment is covered with 2 m. of soil and others in which the valley fill is several hundred meters deep.

On ascending a bajada a gradual change in the vegetation is observable. The stand of plants becomes thicker, the stature greater, the number of trees and large cacti increases, and new species make their appearance. The distance from the base of the mountain at which these changes begin, and the extent of the change, are dependent on the rainfall and the character of the detrital material. Under rainfall of 100 mm. or less, on soil of light texture, the change is least but is still manifested, as may be seen in the Coxcomb and Palen Mountains in California, and in the Sierra Pinta in Baja California. Under rainfall of 150 to 200 mm. on granitic outwash, the change is greater, as in the Harcuvar and Harquahala Mountains in Arizona. In general the amount of change is directly proportional to the size of the mountain from which the bajada descends.

The distinction which is here made between intermont plains, lower bajadas, and upper bajadas is merely the recognition of three phases in a very gradual change of vegetation which accompanies the equally gradual change in soil conditions. The character of the vegetational change is such as to indicate clearly that the water supply for plants grows better as the bajada is ascended. There is an increase in rainfall on going from the center of a valley toward a mountain mass. Added to this initial advantage, the soils of upper bajadas are better suited to the penetration and retention of moisture than are those of lower bajadas and plains. Another feature of the upper bajadas which operates to increase the density and variety of the vegetation is the very coarse character of the soil. Large stones on and near the surface provide the root anchorage which is important for tall, massive cacti. The coarse texture of the soil and good surface drainage obviate the danger of overwetting and poor aeration after periods of heavy rain. The stony surface favors in several ways the establishment of young perennials.

On the ascent of a bajada, the first indications of the change from the lower to the upper type of vegetation are the occurrence of *Olneya tesota* and *Cercidium floridum* or *C. microphyllum* away from streamways, the appearance of *Carnegiea gigantea*, and greater abundance of *Fouquieria splendens*, *Opuntia echinocarpa*, *Ferocactus acanthodes*, and *Acacia Greggii*. *Larrea* continues to be abundant but is no longer the predominant plant. *Franseria dumosa* is still abundant and of greater size, but in many localities is outnumbered or replaced by *Franseria deltoidea*. The number of species and individuals of small perennials gradually increases, and a larger number of plants are found which are mainly confined to the shade of trees. The margins of streamways are lined more heavily by trees

and shrubs than on the lower bajadas, but are less conspicuous than they are in the midst of the pure stands of *Larrea* and *Franseria*. When the composition of the vegetation of upper bajadas is compared with that of streamways on the lower bajadas, it is evident that the plants of the latter habitat are mainly a group of representatives of those found in the former. The slight betterment of soil-moisture conditions found in the two habitats is marked by the appearance of many of the same species. For *Olneya*, *Cercidium*, and *Prosopis* the streamsides of the lower bajadas and plains are a more favorable habitat, at least after initial stages of establishment, than the rocky and more shallow soils of upper bajadas, if favorableness may be judged by the maximum size which these trees attain. *Carnegiea*, *Lemaireocereus*, and the large species of *Opuntia* do not descend along the streamways into the lower bajadas, where soil-moisture conditions are not so favorable for shallow-rooted plants. Certain common plants of the streamways of plains and lower bajadas are rarely found on the upper bajadas, as *Dalea spinosa*, *Baccharis sarothroides*, *Chilopsis linearis*, and *Hymenoclea monogyra*. These find their optimum habitat along streamways which have a heavy bed of sand such as rarely develops on the steeper gradients of the upper bajadas.

In the following list, trees and other plants over 2 m. in height are indicated by figures for their usual range of height. The plants are listed in the order of their relative abundance.

Plants of upper bajadas throughout the Lower Colorado Valley

Larrea tridentata
Cercidium floridum (4–5 m.)
Olneya tesota (4–5 m.)
Fouquieria splendens (3–4 m.)
Carnegiea gigantea (8–10 m.)
Prosopis juliflora var. velutina (3–6 m.)
Cercidium microphyllum (4–5 m.)
Franseria dumosa
Franseria deltoidea
Acacia Greggii
Opuntia echinocarpa
Encelia farinosa
Ferocactus acanthodes

SANDY PLAINS AND DUNES. Nearly one-seventh of the Lower Colorado Valley subdivision of the Sonoran Desert is occupied by sandy plains or dunes. The largest areas lie around the head of the Gulf of California and the Salton Basin; smaller areas lie west of the Mohawk Mountains and southeast of Parker, Arizona. The origin of the sand is not definitely known. It seems probable that it has been largely derived from the broad beaches which are exposed by the wide fluctuations of tide in the Gulf, and from the floor of the Salton Basin. Some of it is of local origin, and perhaps much of it is ultimately derived from the granitic mountains lying within or bordering this subdivision. The sand of the area southeast of Parker has probably been derived from local material. See plates 5, 7.

The greatest development of dunes has taken place west of Pinacate Peak, both along the Gulf coast on Adair Bay and in the interior, culminating in great masses of yellow sand piled against the west base of the peak. A belt of dunes known as "the algodones" extends for 90 km. along the eastern edge of the Salton

Basin, and is crossed by the highway between Yuma and El Centro. Innumerable small dunes occur along the west side of the Salton Basin and along the west coast of the Gulf in Baja California. The small ones are often crescentic in shape, and most of them are gradually moving toward the northeast. These dunes and their vegetation have been described by Rempel (1936), who states that their movement is too rapid for them to become stabilized by plants. Along the eastern edge of the sand in Sonora there are a number of long dune areas projecting eastward over the gravelly plains, indicating the extent to which prevailing westerly winds have been responsible for spreading the sand.

At least four-fifths of the sandy area is relatively level, without local dunes, and has a stabilized surface. In these sandy plains there is little evidence of surface drainage and some evidence of gradual leveling from a less stable condition. Stabilization of the dunes is chiefly due to the coarse grass *Hilaria rigida*, which is not usually abundant on the well stabilized sandy plains. Neither it nor the shrubs have been as important in binding the level surfaces as have the blue-green algae and ground lichens, which form a nearly continuous crust on the most stable plains. The commonest lichens involved are species of *Lecidia* and *Acarospora*, whose periods of vegetative activity must be very brief.

In addition to the plains, in which the sand is from 0.5 m. to many meters deep, there is a large adjacent area of gravelly plain on which a small amount of sand is in perpetual motion over the hard surface and accumulates locally in low miniature dune areas. Such deposits are frequently seen in the malpais areas as well as on the gravel plains. They are abundant in the Castle Dome and La Posa Plains in Yuma County, Arizona, and may be detected by their covering of *Hilaria rigida* or *Opuntia Wrightiana*.

Throughout the extreme northwestern corner of Sonora there is often a close juxtaposition of sand and basaltic rock. Accumulations of sand are common at the windward base of hills (see pl. 6) and have encroached on some of the nearly level malpais fields. The volcanic eruptives have a veneer which is very dark brown or almost black and polished by the moving sand. This results in a strong contrast of color in the landscape, as well as a marked dissimilarity of vegetation.

In the areas of active or moderately active movement the dunes are either devoid of plants or dotted very irregularly with perennials which are usually large examples of their species. When sand accumulates around a plant slowly enough for growth to keep pace with it, the conditions of water supply are improved; but when sand is removed, the plant persists only by reason of its deep-seated root system, or frequently perishes. The only perennials commonly found on moderately active dunes are *Larrea tridentata*, *Franseria dumosa*, *Ephedra trifurca*, *Dalea Emoryi*, *Atriplex canescens*, *Coldenia Palmeri*, *Eriogonum deserticola*, and *Petalonyx Thurberi*. Rare examples of other perennials of the surrounding region may be found on unstable sand, including *Cercidium floridum*, *Hymenoclea monogyra*, and *Chilopsis linearis*. The sporadic distribution of perennials indicates clearly that conditions on unstable sand are more difficult for the establishment than for the persistence of a well rooted plant. This results from the

instability and prevailing dryness of the surface in contrast with the relatively good moisture supply of lower levels. The absence of cacti from deep sand is significant in this connection.

The occurrences of *Hilaria rigida* indicate that it becomes established only on sandy surfaces that have already passed the stage of most active movement. When this stage is reached, *Hilaria*, *Franseria dumosa*, *Dalea Emoryi*, and *Coldenia Palmeri* increase greatly in abundance and the stabilization of the surface is rapidly accelerated.

MALPAIS FIELDS AND VOLCANIC HILLS. The Lower Colorado Valley embraces a large number of areas of varying size and topography in which the surface is occupied by volcanic eruptives which either are recent or have undergone very little erosion or degradation. The largest mountain in this group of areas is Pinacate Peak, which is surrounded by smaller cones, volcanic plugs, and an irregular lava field 50 by 75 km. in maximum extent. The largest malpais area including no large hills is located near Sentinel, Arizona, in the southwestern corner of Maricopa County, and is approximately 25 by 40 km. in maximum extent. Other large areas exist, some of which occupy parts of small ranges of hills while others are nearly level malpais fields. There are innumerable smaller areas.

The volcanic surfaces are exposed in every position from vertical cliffs to nearly level areas. A very common form is the gently tilted mesa, extending for several kilometers at the same gradient, and ending in a scarp at the high end and along one or both of the sides. In southern Yuma County and western Pima County, Arizona, many of the basaltic hills consist essentially of older material and are merely covered with a veneer of basalt from 1 to 2 m. in thickness. This is true of Raven Butte and Sierra Pinta, in southern Yuma County, the latter showing vertical bands of black veneer and the nearly white subjacent material. Road excavation on the highway from Gila Bend to Phoenix has cut through the veneer in two localities (pl. 3, fig. 1), exposing a finely divided highly calcareous soil, and showing the fractured condition of the veneer. In the region south of the Gila River, between Sentinel and Wellton, there are a large number of roughly circular volcanic areas which are highest at the center and fall smoothly at a very low gradient. There is little rock in place at the center although the surface is thickly covered, and the amount of surface rock grows less toward the periphery. Surface deposits of volcanic cinder often exceed the amount of lava. These areas are undoubtedly due to explosive eruptions rather than to the wearing down of small hills.

The character of the vegetation on the volcanic areas is controlled by the three sets of soil conditions associated with the types of surface that have been described. On the edges of the flat areas of explosive origin, the conditions of the plain are slightly modified in the direction of conservation of moisture. On the thin but nearly continuous veneer of impervious rock covering a retentive soil, the runoff penetrates the cracks in the lava and is retained by the soil with extremely

small loss by evaporation. On the thick beds of basalt and other eruptives, a very fine brown clay is formed by weathering and accumulates in pockets of various sizes. The vegetation betrays the slight betterment of moisture conditions around the edges of the malpais fields and the very much better conditions existing on the thick beds of lava. It is not often possible to determine whether trees growing on a volcanic mesa are drawing water from deep pockets of volcanic soil or from the underlying bed of soil which antedated the eruption of the lava.

On the explosive volcanic areas there is great variation in the amount of rock beneath the surface. On the edges of several such areas in Arizona the soil has been found nearly free of the type of stones which thickly cover the surface, but this is not true of the centers of the areas, where one-half to one-fourth of the volume of the substratum is stone.

On the edges of the explosive volcanic areas the vegetation differs little from that of the gravelly intermont plains, but as the center is approached both *Larrea* and *Franseria* become very much less abundant and much smaller, particularly where there is a heavy deposit of cinder. Other perennials characteristic of the gravelly plains and lower bajadas are absent or very sporadic. Small *Olneya* and *Prosopis* trees occur in slight depressions, and single plants of *Fouquieria* appear from place to place.

The extremely rocky and rough surface of the volcanic hills, tilted mesas, and level malpais areas exhibits a great lack of uniformity in its plant cover. There are about 20 trees to the hectare in some localities and none in others. Shrubs and semishrubs may grow abundantly or may be so few that the black-brown rocks give their color to the landscape. Trees are more abundant on small hills and level malpais than on large hills, and semishrubs are commonly more abundant where the rocks are largest and the surface most broken. The vegetation is usually denser at the base of a hill than on its upper slopes, and invariably taller in the shallow canyons and waterways. On the upper slopes of hills there are frequently extensive areas which are nearly bare, or elsewhere stretches of loose rock, with a depth of from one to several meters, with no soil and no vegetation other than the crustose lichens which cover the rocks.

The sporadic occurrence of plants under these conditions is due to the irregular distribution of bodies of soil, and their dissimilar locations with respect to receiving and retaining moisture under conditions of low rainfall and ready evaporation. The relative abundance of trees on small hills and level malpais appears to be due to the existence of soil beneath the basaltic veneer, and the ability of roots to penetrate the cracks in the veneer. The sporadic occurrence of trees and groups of shrubs on slopes is due to the irregular distribution of deep pockets and veins of soil. At the base of a hill and in a place where the rocks are few and large, the pockets of soil receive a heavy runoff, and the depth to which the water can penetrate is usually limited, since rock in place has no such deep cracks as are found in the veneer.

In spite of the lack of uniformity in the physiognomy of the vegetation in the volcanic areas, the same types of community occur over and over again in similar

situations, and the composition of the vegetation is more uniform than its physiognomy. The scarcity of large drainageways and tanks or seepages of water sharply limits the occurrence of trees and other plants of high water requirement.

Plants that are abundant on recent eruptives throughout the Lower Colorado Valley are the following:

Cercidium microphyllum
Olneya tesota
Fouquieria splendens
Encelia farinosa
Larrea tridentata
Heteropogon contortus
Hyptis Emoryi
Krameria canescens
Echinocereus Engelmannii
var. chrysocentrus
Opuntia acanthocarpa
Acacia constricta
Bebbia juncea
Trixis californica
Celtis pallida
Franseria dumosa
Lycium Andersonii
Encelia frutescens
Porophyllum gracile
Dyssodia porophylloides

In the Pinacate lava fields several large perennials are common which are rare or absent north of the Gila River, including *Bursera microphylla*, *Lemaireocereus Thurberi*, *Jatropha cuneata*, and *Solanum Hindsianum*.

Older volcanics. The mountains and hills comprised under this name are those built of rhyolite, andesite, basaltic conglomerate, and all other volcanics except recent basalt. The distinction between "older" and "recent" refers to the stage of physiographic development of their surfaces rather than to their historical sequence. Some of the "older volcanics" are probably contemporaneous with the unmodified areas of basalt.

All the mountains of this class are highly eroded, usually with bare peaks or summits and with very narrow lateral ridges. The surface is either bare rock in place or an accumulation of coarse and unstable angular stones, with a poor development of soil. Since all the mountains and hills of this type in the Lower Colorado Valley lie in the region with less than 150 mm. of rainfall, the conditions for vegetation are extremely unfavorable.

When the older volcanic ranges are viewed from a distance of 2 or 3 km. they appear to be entirely barren of plants, owing to the absence or scarcity of the small trees of the region. On closer approach it is found that there is a very scattered and irregular cover of small perennials and grasses. Even in the canyon bottoms of the ranges near the Colorado River there are few trees, except where a local accumulation of sand or clay has favored *Cercidium floridum* or *Olneya tesota*.

The only plants which are conspicuous on mountain slopes of the most favorable type are *Encelia farinosa* and *Fouquieria splendens*. In many localities the former occurs on the slopes of the mountains and the latter only on the outwash slopes below. In extreme southern Arizona *Lemaireocereus Thurberi* occurs on rocky slopes, usually on a substratum such that it is accompanied by *Olneya* and *Fouquieria*. One of the most ubiquitous plants on the bare slopes is *Hetero-*

pogon contortus. The only cacti that are frequent are *Ferocactus acanthodes* and *Echinomastus Johnsonii*.

Other characteristic perennials of the slopes of the older volcanic mountains are:

Franseria dumosa
Fagonia californica
Krameria canescens
Hyptis Emoryi
Trixis californica
Hilaria mutica
Brickellia atractyloides
Peucephyllum Schottii
Agave deserti

GRANITIC MOUNTAINS AND HILLS. Approximately half of the mountainous part of the Lower Colorado Valley subdivision is composed of crystalline rock, with granite and gneiss preponderant and with smaller areas of schist. The largest granitic ranges are the Harcuvar and Harquahala Mountains and the Gila and Tinajas Altas Ranges, in Arizona; parts of the Chuckwalla and Chocolate Mountains, in California; and much of the great range which bounds the area on the west in California and Baja California. Both these and the smaller masses of crystalline rock vary in their topographic features and differ in the character of the weathering they have undergone. In general the surfaces have weathered more rapidly than in the older volcanic ranges and far more rapidly than in the recent eruptives. The rate of weathering in the granitic ranges has been determined by the durability of the rocks, which are sometimes reinforced by dikes of very resistant quartz. In general there has been sufficient aerial disintegration to provide a soil, and beneath the soil there is an active region of disintegration sometimes extending to a depth of 1 m. or more. Outcrops of rock and dislocated boulders are abundant on the slopes, but are likewise undergoing slow weathering. The soil of the granitic mountain slopes is a coarse sand at the surface, with many large angular fragments, but weathers to a loam at a depth of a few centimeters.

The granitic mountains differ from those previously described in the physiognomy and structure of their vegetation as well as in their flora. Their distinguishing features seem to be closely correlated with the types of soil to which they give rise. The boulder-strewn slopes and the porous surface tend to lessen the runoff, and the structure of the soil is favorable for the retention of water as well as for its penetration into the highly fractured rock beneath the soil.

When the vegetation of granitic mountains is compared with that of near-by volcanic ranges, in localities with nearly identical rainfall, it will be noted that there is a heavier cover on the former and a greater number of large perennials. The cover is far from uniform, being heavier in the bottoms of canyons, near the bases of slopes, and often along definite lines determined by the structure of the rock. There are invariably many small areas of bare rock, cliffs, and boulders, below or around which shrubs are abundant. On granitic mountains the difference in density due to slope exposure is greater than on volcanics so far as nonsucculent plants are concerned. Both large and small cacti are more abundant on slopes of southern aspect, and the nonsucculents on those of northern.

The most conspicuous large perennials of granitic slopes are those indicated

by asterisks in the following list. The vegetation of typical granitic hills in extreme northwestern Sonora is shown in plate 20. The characteristic perennials of granitic mountains are the following, listed in order of approximate abundance:

*Cercidium microphyllum
*Olneya tesota
*Simmondsia chinensis
*Fouquieria splendens
*Jatropha cuneata
Haplopappus laricifolius
Acacia Greggii
Opuntia acanthocarpa
Franseria dumosa
*Carnegiea gigantea
*Bursera microphylla
*Encelia farinosa
Trixis californica
Ephedra viridis
Agave deserti
Lemaireocereus Thurberi
Nolina Bigelovii
Sapium biloculare
Hibiscus denudatus
Galium stellatum

Arizona Upland

(Crassicaulescent Desert. Cercidium-Opuntia Region)

The crassicaulescent desert of the Arizona Upland occupies the inner and more elevated part of the northern half of the Sonoran Desert. Its greatest width is 250 km. in the latitude of Tucson. In its northwestern extension along the foothills of the Colorado Plateau and in its southern extension into Sonora the area narrows to a width of 50 km. or less. The elevation rises gradually from 150 m. at Parker and 335 m. at Phoenix, Arizona, to 950 m. at sections of its boundary near Tucson, Arizona, and Magdalena, Sonora. Approximately 25 per cent of the total area is occupied by hills and mountains. North of the international boundary the drainage of the Arizona Upland is into tributaries of the Colorado; south of the boundary it is carried by Río Magdalena, Río Sonora, and their tributaries. Along the lower courses of the Santa Cruz and Gila Rivers there is a large area of outwash plain in which hills are few and widely spaced.

The rainfall in the Arizona Upland is 125 mm. at Parker and 225 mm. at Ajo, Arizona, and 250 mm. at Altar, Sonora, all these localities being near the lower edge of the area. At Tucson the annual rainfall is 275 mm. and at Magdalena, Sonora, 325 mm., these stations being near the more elevated edge of the subdivision. At the northern end of the area there is a slight preponderance of winter rain over summer, in the center of the area there is approximate equality between them, and at the southern end there is a preponderance of summer rain.

The vegetation of the Arizona Upland is an open stand of microphyllous shrubs and trees with a strong admixture, in certain habitats, of succulents and plants of other types. In the broadest valleys the vegetation is almost as open as on the better-covered gravelly plains of the Lower Colorado Valley. In other situations the cover is heavier, occupying from 20 to 60 per cent of the surface. The broad valleys have a simple vegetation, in which *Larrea* is strongly dominant, with *Franseria dumosa* or *F. deltoidea* occupying a subdominant place. The number of infrequent plants associated with these is greater than in the Lower Colorado

Valley. On coarse outwash plains and slopes *Franseria deltoidea* is usually strongly dominant as to number of individuals, forming the matrix in which *Larrea* is usually likewise abundant, and in which scattered individuals of *Cercidium microphyllum*, *C. floridum*, *Olneya tesota*, and *Prosopis juliflora* var. *velutina* occur, as well as various types of cacti. On the most favorable upper bajadas the number of trees increases, but they never occupy more than 15 per cent of the surface. Under the best conditions for trees the matrix of low shrubbery is usually thinner and broken, and the larger cacti are more abundant.

The Arizona Upland has a maximum length of 650 km. and a north-and-south extent nearly as great as that of the Lower Colorado Valley, yet there is a greater uniformity in the composition of the vegetation in the former area than in the latter. A large number of species are found only in the northern or the southern end of the Arizona Upland; only a few of these play a dominant or subdominant role in the vegetation, except a few species found only west of Wickenburg, Arizona. Owing to the physical features, the vegetation in the Arizona Upland is relatively homogeneous. There are few sharp contrasts in the nature of the surface due to the mineralogical character of the rock, and no large deposits of sand. Throughout the area there are contrasts between the vegetation of volcanic hills and soils and that of granitic ones. With this exception, the differentiation of the vegetation is to be attributed to gradient of slope, depth of soil, physical texture of soil, and surface conditions affecting infiltration. These conditions are closely correlated with the physiographic status of a locality, and result in the consistent repetition throughout the area of closely similar habitats occupied by closely similar vegetation.

The physiographic units with which the vegetation shows close correlation in the Arizona Upland are: plains and lower bajadas; upper bajadas; the slopes of hills and mountains; and streamways. There are some features which distinguish hills and upper bajadas derived from volcanic mountains from those of granitic material. Also the northern and southern ends of the area merit separate treatment.

PLAINS AND LOWER BAJADAS. The plains which border the lower courses of the Gila and Santa Cruz Rivers in this subdivision fall toward the streams at a gradient of 4 to 8 m. per kilometer. Elsewhere, and particularly near the larger mountains, the gradient is steeper, but there are no localities in which lower bajadas are tilted more than 12 m. per kilometer. The soil is commonly a loam or sandy loam, including much coarse gravel, which has a tendency to accumulate on the surface. The structure of the soil is variable, sometimes containing lenses of sand or fine alluvium. Throughout the Arizona Upland the surface is underlain at varying depths by a calcareous hardpan, or caliche, which occurs near the surface as one or more hard, impervious layers, and at a depth of 1 to 3 m. appears as a soft, continuous mass, with included stones, often extending to a depth of several meters. The part played by caliche in the infiltration and evaporation of soil water and in the distribution of roots has been described

by Shreve and Mallery (1933). The visible uniformity of the surface and soil of the plains is matched by the continuity of the vegetation, which is broken only by the bands of larger and more close-set plants along the drainageways. Through the dominance of *Larrea* the vegetation is given a uniform height of 1.5 to 2 m.; the coverage varies from 10 to 20 per cent. The commonest associates of *Larrea* which reach its own or greater height are *Acacia constricta*, *A. Greggii*, and *Prosopis juliflora* var. *velutina*. Away from streamways these plants rarely greatly exceed *Larrea* in height. Several species of cylindropuntia are also locally subdominant, *Opuntia versicolor*, *O. arbuscula*, and *O. spinosior* rarely exceeding the general height, but *O. fulgida* and *O. fulgida* var. *mammillata* often greatly exceeding it.

On the largest plains, where the soil contains the smallest amount of coarse material and where the surface is without a continuous cover of gravel, the spaces between bushes are bare or nearly so. Semishrubs, with a height of 2 to 5 dm., occur with great irregularity. The commonest of these are *Franseria dumosa*, *F. deltoidea*, *Krameria canescens*, *Zinnia grandiflora*, and *Haplopappus Hartwegii*. Grasses are scantily represented except in poorly drained areas of heavy soil, in which well closed stands of *Hilaria mutica* are found. Under *Larrea*, and reclining on its limbs, *Muhlenbergia Porteri* is abundant where there has not been recent grazing. Near the flood-plain edge of the gravelly plains bushes of *Prosopis* are often abundant, and on alkaline soil *Atriplex canescens* forms nearly pure stands.

Between the Gila and Salt Rivers, south of Chandler, Arizona, is a plain of very low gradient with deep loam soil. This has largely been brought under cultivation since 1930, but originally bore a heavy cover of *Atriplex polycarpa* and an open forest of *Carnegiea gigantea* (pl. 12). This is the only locality in which *Carnegiea* is known to occur abundantly on a relatively fine, rock-free soil.

West and southwest of Wickenburg there are a number of depressions, all less than 1 km. in diameter, in which *Hilaria mutica* forms a close stand, free of bushes and trees. The only perennial growing with this grass is the erect platyopuntia *O. chlorotica*, which gives the community an appearance like that of the cactus-acacia grassland which is widespread in Zacatecas and adjacent states. In the surrounding areas *O. chlorotica* is infrequent. Its most widespread habitat is the rocky slopes of the mountains which fringe the Sonoran Desert on the north and east, where it is rarely as abundant as in the small areas of *Hilaria*.

Throughout the plains and lower bajadas the monotony of the vegetation is sometimes broken by the occurrence of isolated plants of species which are abundant on the upper bajadas, especially *Fouquieria splendens*, *Ferocactus Wislizenii*, *Carnegiea gigantea*, *Condalia lycioides*, and *Celtis pallida*. Much more infrequent are a few species found in no other habitat in the region, including *Holacantha Emoryi*, *Koeberlinia spinosa*, and *Bumelia occidentalis*.

In the valley of the Bill Williams River the areas of plain and lower bajada are limited in extent. The region north of the river is rugged and rolling and bears the upper bajada type of vegetation. South of the Bill Williams and north of the Harcuvar Mountains is Butler Valley, a plain 30 by 40 km. in extent in

which there is one of the heaviest and finest stands of *Larrea* in the Sonoran Desert.

South of Santa Ana, Sonora, the lower bajadas differ from those farther north in the greater number of small trees of *Prosopis* and *Cercidium* growing with the prevailing *Larrea*, and in a stronger representation of grasses.

UPPER BAJADAS. Approximately half the area of intermont plain in the Arizona Upland is here designated as upper bajada. It includes the pediments which often surround the mountains, and a varying percentage of the outwash slope which falls at uniform gradient toward the central drainageway. Where the mountains are widely spaced, the zone of upper bajada may extend only one-fifth of the distance from mountain to drainageway. Where the mountains are closely spaced, the physical and vegetational features of the upper bajada may extend down the entire slope to its base. The boundary between upper and lower bajada, as already stated, is a very broad and indefinite one. Also the vegetation of the upper bajada, especially on pediment, approaches closely that found on the slopes of hills and mountains.

The areas of upper bajada encircle all the isolated mountains in the central part of the Arizona Upland, and include nearly all the intermont areas south and west of the Salt River and north of the Altar River. Whereas the soil of the lower bajadas is often a mixture of material from various sources, that of the upper bajadas is derived from a single mountain range, or part of such mountain, and commonly has distinctive physical features attributable to the character of the rock from which it is derived. The prevailing material from which the soils of the upper bajadas have come consists of basalt, andesite, rhyolite, and volcanic conglomerate, resulting in soils of coarse texture with many angular fragments on and beneath the surface, and very generally cemented by calcareous hardpan. The upper bajadas on which the soil has been derived from rocks of granitic types have a deep, sandy loam, without calcareous hardpan. Much coarse sand is included in the granitic soil and accumulates on the surface, where it clogs the drainage and results in rapid lateral migration of the streamways. Large stones and coarse gravel are relatively infrequent in the soil and on the surface. Such soil has sufficient clay to become very hard when dry, but is friable when moist.

The vegetation of upper bajadas in the Arizona Upland is the highest type found in any part of the Sonoran Desert north of the international boundary and outside the moist flood plains. There are more large perennials per unit area than in any other group of habitats, the stature of the large perennials is greater, the number of associated smaller perennials is greater, and the number of species is larger. The number of species of perennials reaching a height of 1 m. or more is rarely more than 20 in any one locality, and their relative abundance varies from place to place. The most abundant of the 20 (*Larrea*, *Cercidium microphyllum*, *Opuntia versicolor*, *O. Engelmannii*, *Fouquieria splendens*, *Lycium Andersonii*, *Condalia lycioides*, *Celtis pallida*, and *Prosopis juliflora* var. *velutina*) are present on nearly every square kilometer of the area. *Carnegiea* is far less numerous

than the above plants, but its height makes it a conspicuous element in the vegetation. *Fouquieria* is particularly abundant on the pediments and very coarse soil. *Larrea* is more abundant on level areas and benches than on the steeper slopes with coarse, shallow soil. As the bajada is ascended, *Cercidium* increases in abundance, and *Prosopis* more frequently reaches the size of a small tree.

With particular reference to the broad part of the Arizona Upland lying between the Salt River on the north and the Altar River on the south, the following perennials more than 1 m. in height are characteristic of the upper bajadas:

Cercidium microphyllum
Larrea tridentata
Acacia constricta
Fouquieria splendens
Prosopis juliflora var. velutina
Opuntia versicolor
Olneya tesota
Opuntia Engelmannii
Acacia Greggii
Opuntia fulgida
Celtis pallida
Lycium Berlandieri
Ferocactus Wislizenii
Simmondsia chinensis
Ephedra trifurca
Opuntia spinosior
Lycium Fremontii
Condalia lycioides
Forestiera neomexicana
Condalia spathulata

The smaller perennials accompanying the above are:

Franseria deltoidea
Encelia farinosa
Calliandra eriophylla
Opuntia leptocaulis
Zinnia grandiflora
Opuntia phaeacantha
Krameria glandulosa
Coldenia canescens
Menodora scabra
Psilostrophe Cooperi†
Brickellia Coulteri
Parthenium incanum
Muhlenbergia Porteri
Sphaeralcea Gooddingii var. grossulariaefolia
Jatropha cardiophylla
Trixis californica
Tragia ramosa
Mammillaria microsperma
Hibiscus denudatus
Ayenia microphylla
Dalea Parryi
Abutilon incanum
Polygala macradenia
Porophyllum gracile
Hibiscus Coulteri
Haplophyton cimicidium

In some of the warmest situations along the western edge of the Upland between Gila Bend, Arizona, and Caborca, Sonora, there are other dominant and subdominant species, most of which are here at the northern limit of their ranges and are not found elsewhere in the United States. These include *Lemaireocereus Thurberi*, *Bursera microphylla*, *Ferocactus Covillei*, *Lophocereus Schottii*, *Jatropha cuneata*, and *Bumelia mexicana*.

†This and several other species grow as annuals if rainfall is abnormally low, but become perennials of short duration if the conditions for growth are more favorable.

The northwestern arm of the Arizona Upland west of Wickenburg is a rugged area of low mountains and pediments with few expanses of plain even along the Bill Williams River. The general features of the vegetation are those of the central part of the subdivision. The stature and density are similar and the composition is somewhat richer. A number of plants playing an important role in the vegetation occur in the Sonoran Desert only in this small section. Several of them are common in the Mojave Desert and are here at their southeastern limit. Others are dominants of the adjacent arid woodland which extend only a few kilometers into the desert in close association with its characteristic plants. Near Wikieup and Signal, Arizona, there are many localities in which *Carnegiea*, *Cercidium*, *Larrea*, and *Encelia* grow with *Yucca brevifolia*, *Juniperus utahensis*, *Quercus turbinella*, and *Berberis haematocarpa*. Exit from the desert on the rolling ground southwest of the south end of the Hualpai Mountains is indicated by a slight increase in stature and density of the plants, by the disappearance of *Cercidium*, *Larrea*, *Carnegiea*, *Encelia*, and *Simmondsia*, and by the dominance of *Yucca brevifolia*, *Juniperus utahensis*, *Yucca baccata*, and *Quercus turbinella* (pl. 13).

The following plants are found in the Sonoran Desert only in the northern arm of the Arizona Upland, where they are commonest on upper bajadas, pediments, and hillsides. They are all either abundant or conspicuous elements in the vegetation.

Yucca brevifolia
Juniperus utahensis
Acamptopappus sphaerocephalus
Thamnosma montanum
Ephedra viridis
Yucca baccata
Opuntia basilaris
Canotia Holacantha
Halliophytum Hallii
Salazaria mexicana
Nolina Bigelovii
Quercus turbinella
Agave deserti
Aster abatus

The southern end of the Arizona Upland, lying south of the Altar River, is similar to the northern arm in its rugged topography and low relief. It lies between the oak-clad mountains which bound the desert and the plains which extend to the Gulf of California. The surface is mainly hill, pediment, and upper bajada, with small areas of lower bajada and flood plain.

In the southern arm of the Upland the stature of the vegetation is similar to that in the main area, but the density is slightly greater, particularly that of the shrubs. The dominance is still held by *Cercidium*, *Opuntia*, and *Carnegiea*, but the composition is different from that in the central area. The dominant perennials are:

Cercidium microphyllum
Prosopis juliflora var. velutina
Acacia constricta
Opuntia Engelmannii
Opuntia spinosior
Larrea tridentata
Carnegiea gigantea
Cercidium floridum
Celtis pallida

(*Continued on following page*)

Encelia farinosa
Olneya tesota
Opuntia fulgida
Jatropha cordata
Acacia Greggii
Dodonaea viscosa
Opuntia versicolor
Mimosa laxiflora
Condalia spathulata
Croton sonorae
Lycium Andersonii
Franseria cordifolia
Coursetia glandulosa
Caesalpinia pumila

South of the Altar River it is noticeable that slight topographic differences affect the vegetation and flora more than is the case farther north. This holds true whether it is moisture or temperature conditions that are concerned.

In a short and very abrupt box canyon on the southwest face of Sierra Babiso, about 35 km. southeast of Magdalena, is a heavy stand of the palm *Sabal uresana*. The soil of the floor of the canyon is kept moist by springs, and the shade of the palms is so dense that the only accompanying plants are small turgescent herbaceous perennials, including mats of *Tradescantia semisomna*; the lower walls of the box are clothed with mesic ferns and *Rhus choriophylla*.

About 15 km. northeast of Ímuris, Sonora, the Magdalena River traverses a canyon about 7 km. in length at an altitude of 1000 m. On the steep but well clothed lower slopes of the canyon a group of plants of southern range is found, few of which are known farther north and several of which are not known for 200 to 300 km. to the south. There is undoubtedly a marked temperature inversion here, as in all situations of the same character (see Shreve, 1912), the walls of the canyon being steep and the air-drainage area being large and of higher elevation. Under such conditions the lowest winter minima on the slopes above the cold-air flow would be higher than on other slopes in the vicinity, as well as higher than the minima above a more shallow flow of cold air.

Among the plants detected in Magdalena Canyon are:

Acacia Farnesiana
Acalypha subviscida
Iresine paniculata
Cocculus diversifolius
Phaulothamnus spinescens
Croton ciliato-glandulosus
Gronovia scandens
Solanum Grayi
Milleria quinqueflora
Tillandsia recurvata
Pseudabutilon sonorae
Tithonia Thurberi
Rothrockia cordifolia
Acalypha polystachya
Elytraria imbricata
Senecio saligna

Hills and mountain slopes. There are many localities in the Arizona Upland where the vegetation of the hills and lower mountain slopes does not differ in any respect from that of the bajadas and pediments which the slopes overlook. This is particularly true along the inner edge of the Upland, where a high percentage of the surface is covered with thin residual soils. The physiognomy of the slope vegetation depends primarily on the kind of rock involved and the manner in which it has weathered, since this determines the amount, depth, and continuity of the soil, as well as its capacity for infiltration and retention of water. In general,

the slopes which have the most uniform surface have the most uniform and evenly spaced vegetation. Under these conditions the stand of shrubbery is very open and the trees few or absent. On slopes with a rough surface, broken by large boulders, small escarpments, or extrusions, the plants are irregular in spacing and stature and each species is confined to sites of a definite type. On rough slopes the stature of the largest plants greatly exceeds that on the uniform slopes.

On recent eruptives below 750 m. elevation, *Larrea* is dominant on the lower slopes of many hills and mountains in this area. At higher elevations, and on other soils, particularly granitic loam, *Larrea* is consistently absent from the slopes. The occurrence of *Cercidium microphyllum* is the reverse of this. It reaches its maximum size and density on granitic loam slopes and upper bajadas near the inner edge of the Arizona Upland, and extends up the larger mountains to 1000 to 1300 m. above the edge of the desert.

The lower slopes throughout the central part of the Arizona Upland are dominated by *Cercidium microphyllum*, *Fouquieria splendens*, *Carnegiea gigantea*, *Encelia farinosa*, *Acacia constricta*, and several cylindropuntias and platyopuntias. On upper slopes *Cercidium floridum* is more abundant than *C. microphyllum*, and it is not there confined to the banks of streamways as it is on the floor of the desert; *Prosopis juliflora* var. *velutina* becomes more abundant as a small tree of 2 to 3 m.; and *Carnegiea* and *Fouquieria* are closely restricted to warm sites. In the rugged area drained by the Gila River, *Simmondsia chinensis* is strongly dominant on many north slopes. At desert levels in such situations it is not uncommon to find large perennials which are characteristic and abundant at higher elevations, for example *Dasylirion Wheeleri*, *Haplopappus laricifolius*, *Vauquelinia californica*, *Lippia Wrightii*, *Rhamnus ilicifolia*, and *Quercus turbinella*. Through a vertical range of 400 m. above the limit of the desert there is a gradual disappearance of characteristic desert plants. Isolated individuals or colonies of certain ones may be found as high as 2000 m. The transition from purely desert communities to desert grassland, xeric woodland, or chaparral invariably takes place at lower elevations on granitic slopes than on volcanic eruptives.

A faithful description of the vegetation of a basaltic hill in the Arizona Upland, near Tucson, was published by Spalding (1909), including lists of all the known species found in the several habitats of the area. The vegetation of the desert slopes of the Santa Catalina Mountains, near Tucson, was described by Shreve (1915), who also gave an account of the transition from desert to xeric woodland.

The plants which are most characteristic of hill and mountain slopes and most generally distributed throughout the Arizona Upland are the following:

Cercidium microphyllum
Encelia farinosa
Fouquieria splendens
Acacia constricta
Celtis pallida
Opuntia versicolor
Cercidium floridum
Carnegiea gigantea
Condalia spathulata
Calliandra eriophylla
Jatropha cardiophylla

(*Continued on following page*)

Opuntia leptocaulis
Menodora scabra
Dalea Parryi
Ferocactus Wislizenii
Heteropogon contortus
Krameria canescens
Muhlenbergia Porteri
Brickellia Coulteri
Parthenium incanum
Prosopis juliflora var. velutina
Janusia gracilis
Ayenia microphylla
Opuntia Bigelovii
Ephedra trifurca
Dyssodia porophylloides
Trixis californica
Lippia Wrightii
Hibiscus Coulteri

In addition to the plants listed, there are over 300 perennials which either occur infrequently and locally or else are very inconspicuous elements of the vegetation. On very rough slopes, particularly those of northern or eastern aspect, *Selaginella rupincola* forms an almost continuous carpet, gray and inconspicuous in the dry months but a vivid deep green during the summer rains. Several grasses which are commonly annuals (notably *Aristida adscensionis*) often find the conditions favorable enough to live through two or more rainy seasons. Under ledges of rock and in the shade of large trees are found small xeric ferns, which produce fresh fruiting fronds twice a year. The most abundant of these are *Cheilanthes Lindheimeri*, *C. Pringlei*, *C. Wrightii*, *Notholaena sinuata*, and *Pellaea mucronata*.

In the northern arm of the Arizona Upland the character of the physiography is such as to obscure the contrast between pediments and slopes, and their vegetation is often identical. On the steepest slopes, however, the vegetation is more open than in the central part of the Upland, and large trees of *Cercidium* and *Olneya* are rare. Near the upper limit of the desert the influence of slope exposure is pronounced. The familiar phenomenon of "inversion of zones" may be noted in many localities, where steep south-facing slopes overlook bajadas with marginal xeric woodland vegetation but are themselves clothed with desert plants.

Nearly all the plants listed as characteristic of slopes in the central part of the Arizona Upland are also found in the northern arm, although several are less frequent, and *Opuntia versicolor*, *Jatropha cardiophylla*, *Ferocactus Wislizenii*, and *Janusia gracilis* appear to be absent. A few species are found abundantly in the northern arm which are not known elsewhere in the Upland:

Eriogonum fasciculatum
Ferocactus Lecontei
Nolina Bigelovii
Crossosoma Bigelovii var. glaucum
Echinocereus Engelmannii
Rhus choriophylla
Galium stellatum
Ditaxis lanceolata
Physalis crassifolia
Notholaena Parryi

On going from the central Arizona Upland to its southern end, little change in the slope vegetation is encountered except along the eastern edge of the desert south of Magdalena, Sonora. The principal differences are in certain regions where the shrubbery is very heavy, and others where perennial grasses are abundant. Also there are a few important differences in composition.

There appears to be no definite relation between the density of the open stands of *Cercidium* and *Olneya* and the number of shrubs occurring in the intervals between them. *Larrea* is almost completely absent from slopes in this region, and *Encelia* is here more common on the bajadas and plains than on the hills. The increasing density of the interarboreal shrubbery is not due to greater abundance of the shrubs found farther north so much as it is to the appearance of southern species not found in Arizona or else uncommon there. The principal shrubs in this group are *Dodonaea viscosa*, *Caesalpinia pumila*, *Franseria cordifolia*, *Croton sonorae*, *Jatropha cardiophylla*, *Phaulothamnus spinescens*, and *Tecoma stans*.

STREAMWAYS. In all parts of the Arizona Upland the banks and margins of streamways show vegetational differences from the general surface, therein contrasting with such habitats in the most arid parts of the North American Desert. The differences may be only in the density and size of species common elsewhere, or may consist in the presence of distinctive species. Usually both these features appear along small drainageways.

The converging ribbons of denser vegetation along the small streamways are very conspicuous when a plain or bajada is viewed from an elevation or from the air (see pl. 8). As soon as a drainageway becomes large enough to have interrupted deposits of sand in its bed, the marginal vegetation begins to be heavier. When the sandy bed becomes nearly continuous and reaches a width of 1 to 2 m., the marginal vegetation becomes still more dense; *Larrea* responds notably in height and bulk to the slight improvement in moisture conditions; *Prosopis juliflora* var. *velutina*, *Acacia constricta*, and *A. Greggii* contribute more than any other plants to the increased density. Species then found along the streamways but not away from them are *Cercidium floridum*, *Condalia spathulata*, *Lycium* spp., *Baccharis sarothroides*, *Anisacanthus Thurberi*, and *Franseria ambrosioides*. Several species of *Opuntia*, notably *O. versicolor*, *O. spinosior*, *O. leptocaulis*, and *O. arbuscula*, retain their relative abundance along the streamways.

Broad streamways filled with sand to depths as great as 1 to 3 m. present ideal conditions for a greater soil-moisture supply than that prevailing away from their banks. The runoff into the sandy beds greatly increases the potential water supply at the expense of the upland. The infiltration is rapid and deep. The quick drying of the surface sand retards the loss of water. The presence of large trees of *Cercidium*, *Olneya*, and *Prosopis* along sandy streamways forms a sharp contrast with the low and open stands of *Larrea* which prevail a few meters beyond the edge of the sandy reservoirs of moisture.

The vegetation along larger streamways is determined by the character of their storm floods and by the distance from the headwaters or parent mountain of the stream. There are very few complacent streams in the Arizona Upland and none that flow for more than 6 or 7 months of the year. All of them are subject to violent floods which last only a few hours or a few days and are often very destructive to the marginal vegetation. Flood plains have developed along most of the large streamways, but are rarely more than a few hundred meters

in width. The flood bed of the stream commonly lies below the level of the flood plain at a depth ranging from 1 or 2 m. to as much as 12 or 15 m. in exceptional cases. It is believed that the cutting of deep channels by desert streams has taken place largely within the past seventy-five years and is due to disturbance of the surface of the catchment basin by heavy grazing (see Bryan, 1925). Nevertheless, a limited amount of channel cutting has always been a part of the normal history of desert streamways, alternating with periods of lateral cutting, and bringing about constant readjustment of level and equalization of gradient.

Along large streamways the vegetation of the margins and flood plains is determined by the character of the soil, which is roughly of three types. Near the parent mountain the stream bed and the flood-plain soil are full of boulders, and this condition may extend for a few kilometers beyond the base of the mountain. Where the flood plain has been built up over a long period by wide and slowly moving floods, the soil is a fine alluvial clay. This type of flood plain is found along streamways which have a low gradient of fall, unconfined banks, and a heavy seasonal flow from a large drainage basin. The third type of flood plain is the product of flash floods. The surface is sandy, and the subsoil may be sand or a heavier soil laid down under different conditions in the past. Sandy flood plains are found where the channel is shallow or absent and the floods are infrequent, violent, and usually from sources far upstream.

The vegetation of the boulder flood plains is highly mesic and closely related to that of the encinal. It is richly supplied with water at the same time that it is subjected to maximum temperatures as great as those of the floor of the desert. The extent of the bands of mesic vegetation is sharply limited on the sides by contrasting slopes with xeric plants, and gradually wanes downstream as the moisture supply decreases. Between 750 and 950 m. elevation in all the large canyons of the mountains which border the inner edge of the Arizona Upland there is a mingling of encinal and desert trees. The former include *Quercus Emoryi*, *Q. arizonica*, *Q. oblongifolia*, and *Q. hypoleucoides;* the latter include *Populus Fremontii*, *Salix Gooddingii*, *Fraxinus velutina* var. *Toumeyi*, *Juglans major*, *Prosopis juliflora* var. *velutina*, *Platanus Wrightii*, *Sambucus mexicana*, and *Celtis reticulata*. At this elevation the oaks rarely extend beyond the mouth of the canyon, as they do in similar situations at higher elevations.

The shrubs and other perennials which characterize the boulder flood plains are:

Celtis pallida
Acacia Greggii
Franseria ambrosioides
Baccharis sarothroides
Hymenoclea monogyra
Opuntia versicolor
Dodonaea viscosa var. angustifolia
Baccharis viminea
Coursetia glandulosa
Rhamnus californica subsp. ursina
Lycium spp.

After the largest streams of the Arizona Upland have traveled a few kilometers from the base of the mountains in which they originated, there is a great reduction

in the number of common trees and shrubs and an approach toward the characteristics of either the alluvial or the sandy type of flood plain. *Prosopis* becomes the dominant tree, and *Populus* and *Salix* are frequent. All the trees occur in belts, in irregular groves, or as isolated trees.

The alluvial flood plains of the Arizona Upland are one of the most favorable desert environments in respect to water supply and depth and texture of soil. The original vegetation was a nearly pure stand of large trees of *Prosopis juliflora* var. *velutina*. These trees long constituted the only source of good fuel in the region, and the soil on which they grew was the most fertile, tillable, and easily irrigated land. For these reasons nearly all the alluvial flood plains have been denuded of trees or now have open stands of small second- or third-growth trees which have sprung from suckers from the original stumps. In some places there is evidence that the changing regimen of the rivers has covered the clay bottoms with sand and converted the flood plains from the alluvial to the sandy type.

The splendid forests of *Prosopis* which once grew in many localities along the Gila, Santa Cruz, San Pedro, and Magdalena Rivers have given place to fields of cotton, alfalfa, or barley. A few small virgin stands of *Prosopis* may still be found on the San Pedro River above Redington, Arizona, on the Altar River near Tubutama, and on the San Miguel River above Horcasitas, Sonora. In these stands the trees are 15 to 18 m. in height with a trunk diameter of 12 to 15 dm. The finest groves that have been examined are nearly pure, with a few *Acacia Greggii* and *Fraxinus velutina* var. *Toumeyi*, and have a clean floor with few shrubs and herbaceous plants. The edges of the *Prosopis* groves and the places disturbed by natural or human agency are dense jungles of young *Prosopis*, *Acacia Greggii*, *Celtis pallida*, *Condalia lycioides*, and *Lycium* spp. In these jungles there are more vines than in any other desert habitat. The commonest is *Clematis Drummondii*, which flourishes in sun and shade. Other climbers found chiefly in this habitat are *Vitis arizonica*, *Funastrum cumanense*, *Echinopepon Wrightii*, and *Cocculus diversifolius*.

The sandy flood plains lie near the level of the stream bed and are subject to overflow at times of heavy rain. They are virtually a seldom used part of the stream bed, submerged only by rapid torrents which overflow the bed itself, whereas the alluvial flood plains were originally built by slowly moving widespread floods in their depositional phase. The substratum of the sandy flood plains is a mixture of sand and coarse, partially worn gravel. The conditions are very unfavorable for the establishment of trees. Here and there are individuals of *Populus*, *Salix*, or *Prosopis*, which usually show distortion and root exposure due to the floods.

The dominant plants of the sandy flood plains throughout the Arizona Upland are *Hymenoclea monogyra* and *Baccharis sarothroides*, both of which are shrubs of rapid growth and of such habit that partial burial by sand does not interfere with their growth. On the Bill Williams River in western Arizona the sandy flood plain is overflowed almost annually and is exceptionally well supplied with moisture. There the commonest plant is *Baccharis viminea*. On the Gila River

the natural conditions have been much modified by construction of the Coolidge and Gillespie Dams, and there has been a steady decrease in the extent of sandy flood plain in recent years. In many localities on the Gila River the introduced *Tamarix parviflora* has replaced the native shrubs. The only common woody associate of *Hymenoclea* and *Baccharis* in Arizona is the slender shrub or small tree *Chilopsis linearis*. The semishrub *Franseria ambrosioides* is also abundant, as well as the winter-active, tuberous-rooted *Rumex hymenosepalus*.

Plains of Sonora

(Arbosuffrutescent Desert. Olneya-Encelia Region)

The Plains of Sonora constitute the smallest and least diversified of the vegetational subdivisions of the Sonoran Desert. They occupy an important place in the North American Desert, however, because they are the southern termination of the very arid type of continental desert which extends north to eastern Oregon, and in them are found the first manifestations of botanical features which characterize the west coast of Mexico far to the south.

Over most of the area the impression given by the vegetation is that of a very open forest of small, low-branching trees, with irregularly placed colonies of shrubs which are not tall enough to impair the view, and with large but very widely spaced columnar cacti. The dominants of the Lower Colorado Valley, *Larrea*, *Franseria dumosa*, and *F. deltoidea*, are here of local occurrence. Colonies of *Opuntia* are relatively infrequent. There is a distinct approach toward association of plants which are more uniform in habit than is the case in the subdivisions which have been described. In the Plains of Sonora *Cercidium*, *Olneya*, and *Prosopis* find their optimum conditions and show their maximum size, abundance, and catholicity of habitat. In the central and southern parts of the Plains these trees are joined by a number of subdominants, only one of which, *Bursera microphylla*, extends north of the international boundary. The gradual enrichment of the flora also extends to the shrubs and herbaceous perennials, although not to the ephemerals. In this subdivision low stature, open spacing, and diversity of life forms, which are the cardinal features of the desert, are still prevalent but are beginning to wane.

The northern boundary of the Plains of Sonora is on the long slope which rises from the Río Magdalena southward to the Sierra de la Compañía. The area extends south for about 250 km. to the vicinity of Guaymas. The western edge of the Plains subdivision is a poorly defined transition to the Lower Colorado Valley or to the Central Gulf Coast subdivision at elevations of from 100 to 400 m. and at 30 to 50 km. from the Gulf coast. The eastern edge of the Plains is defined by hilly or mountainous areas lying in the southern extension of the Arizona Upland or in the Foothills of Sonora. The floor of the Plains area reaches its highest elevation of 800 m. at its northeast corner, and the eastern boundary falls to 100 m. at the south.

Only in the proximity of the widely spaced mountains is the gradient of the

intermont plains greater than 1 or 2 m. to the kilometer. The only important rivers crossing the area are the Río Sonora and its tributary the Río San Miguel. Many of the short drainageways originating in the Plains of Sonora flow toward the Gulf of California, but their waters are spread and lost in the Gulf coast region.

The soils are prevailingly of mixed material that has been moved far from its place of origin. The mountains are chiefly volcanic extrusives; a few are granite or gneiss; at least two large groups of hills are limestone, and small exposures of limestone are found in many places. The distinction between upper and lower bajadas which has been described for the Arizona Upland is only of local importance here, where there is neither physical nor vegetational basis for its recognition. Sections of the soil exposed by river channels show it to be a loam or clay loam which is deep, relatively uniform, and poor in large stones. Caliche is present along the western edge of the region, but is far less general in occurrence than it is in the Lower Colorado Valley and Arizona Upland.

Both the vegetation and the flora of the Plains of Sonora are influenced by the position of the area at the threshold of the transition from desert to thorn forest. So many species appear which are absent from the northern subdivisions that the contrast between the northern and southern ends of the area is far greater than the contrast in the same distance in the Lower Colorado Valley from Needles to Yuma, or in the Arizona Upland from Wickenburg to Sonoyta. The gradual enrichment of the flora from north to south and its effect on the composition, structure, and physiognomy of the plant communities is an outstanding feature of the area. There is also the universal contrast between the vegetation of hills and that of plains. The fact that many of the newly encountered plants extend much farther north on the hills than on the plains causes an intermingling of the two principal differentiating features.

Northern Plains region. Throughout the northwestern third of the Plains of Sonora there are numerous areas in which *Larrea* is abundant. Large pure stands are rare, as it is generally accompanied by at least a small representation of *Olneya*, *Cercidium*, *Fouquieria splendens*, and *Encelia farinosa*. Many open areas are encountered in which *Larrea*, trees, and large cacti are absent and shrubs are few. These bare areas commonly have a narrow, irregular form and extend for several kilometers between the well wooded belts along the drainageways.

North of Carbó the vegetation of the Plains of Sonora is little affected by the influx of southern plants. Colonies of *Larrea* alternate with open forests of *Cercidium microphyllum*, *C. floridum*, *Olneya tesota*, *Prosopis juliflora* var. *velutina*, *Fouquieria splendens*, and *Lemaireocereus Thurberi* (pl. 14). The stature of the trees ranges from 4 or 5 m. to 8 or 10 m., and the density is highly variable. The largest trees occur in the heaviest stands, where the coverage is as much as 20 per cent. The smallest trees occur with *Larrea* or on the borders of bare areas, and often number only 5 or 6 to the hectare. The prevailing vegetation is near the average between these extremes. *Encelia farinosa* is the dominant shrub

outside the colonies of *Larrea*. Its height is about 1 to 1.5 m., and its density is rarely so great that its branches interlock. *Encelia* is most abundant in the open, and rarely occurs under wide-spreading trees, although the shade of such trees is always light (pl. 15).

There are no subdominants in the northern part of the Plains of Sonora. Large perennials other than those that have been mentioned are either infrequent or else found in scattered colonies. The most common colonial perennials are *Opuntia arbuscula*, *O. fulgida* var. *mammillata*, and *Lophocereus Schottii*. The trees and large shrubs most often found are:

Acacia constricta (shrub)
Bursera microphylla (tree)
Acacia occidentalis (tree)
Caesalpinia pumila (shrub)
Croton sonorae (shrub)
Jatropha cardiophylla (small tree)
Lycium brevipes (shrub)
Krameria parvifolia (shrub)
Celtis pallida (shrub)
Condalia lycioides (shrub)
Opuntia leptocaulis (slender cylindropuntia)
Coursetia glandulosa (shrub or small tree)
Eysenhardtia orthocarpa (shrub)

On volcanic hills the vegetation is usually somewhat heavier than on the plains, but this is not invariably the case. *Cercidium* and *Olneya* are the dominants on hills as well as plains. *Prosopis* and *Acacia occidentalis* are rarely found on hills in this region. The characteristic population of hills includes:

Cercidium microphyllum
Olneya tesota
Fouquieria splendens
Lemaireocereus Thurberi
Jatropha cuneata
Opuntia Engelmannii
Bursera microphylla
Croton sonorae
Opuntia Gosseliniana
Celtis pallida
Ferocactus Covillei
Phaulothamnus spinescens
Carnegiea gigantea
Sapium biloculare
Condalia spathulata
Larrea tridentata
Lycium Berlandieri
Echinocereus Engelmannii
Hyptis Emoryi

About 70 km. southwest of Santa Ana is the largest group of limestone hills that has been found in the Plains of Sonora. The highest is Cerro Santa Rosa, which rises only about 400 m. above the basal elevation. The irregular group of hills surrounding Cerro Santa Rosa is maturely dissected and rounded in outline. The vegetation departs radically from that of the volcanic hills both in physiognomy and in composition. The cover is a dense, uniform stand of large shrubs, without *Cercidium* or *Olneya* and with very few cacti of any type. The dominants are *Acacia constricta*, *Caesalpinia pumila*, *Eysenhardtia orthocarpa*, *Fouquieria splendens*, *Condalia spathulata*, *Bursera laxiflora*, *Croton sonorae*, *Tecoma stans*, and *Jacobinia ovata*.

CENTRAL PLAINS REGION. In the central part of the Plains of Sonora between the latitudes of Carbó and Hermosillo there is an increase in the density of the vegetation, but not in its stature. The areas of open forest become greater, except in the west, where colonies of *Larrea* are still frequent. The shrubbery becomes much more continuous and its stature greater than in the northern end of the Plains. There are still many areas with few trees and shrubs, and occasional ones with no large perennials. The ephemerals and summer-active perennials which occupy the open areas as well as the wooded and shrubby ones are abundant in the late summer and usually completely carpet the soil. Grasses often form as much as 75 per cent of this cover, which gives an aspect of abundant verdure after the period of summer rain. By the middle of November all these plants are dead or inactive, changing the tone of the landscape from green to brown, but still serving to prevent the appearance of bareness that is so common in the areas to the north.

In the central third of the Plains subdivision there is a strong enrichment of composition, due to the entry of many plants of southern range. Several of the new dominants and subdominants are plants of striking habit, which serve to maintain the diversity of life forms. The majority of the less common entrants, however, are more alike and nearer to the generalized types that prevail in dry subtropical regions.

The two levels of vegetation formed by trees and by shrubs throughout the northern part of the Sonoran Desert now become less clearly marked. The stature of *Encelia* increases toward the south and away from the Gulf, and many of its associates exceed it in height. Also several woody perennials occur which in height and form are intermediate between shrubs and the small trees of the desert.

The large perennials entering the vegetation in the central part of the Plains of Sonora occur at first singly and far apart, but usually as large, well developed individuals. The fringe of their ranges is not broad, however, and within 30 or 40 km. of the northernmost individuals, most of the species are abundant or even subdominant. The large perennials which quickly take a prominent place in the vegetation are:

Fouquieria Macdougalii
Bursera laxiflora
Cercidium sonorae
Jatropha cordata
Guaiacum Coulteri
Rathbunia alamosensis
Ipomoea arborescens
Jacquinia pungens
Randia Thurberi
Opuntia Thurberi

The entrance of these plants does little to remove *Cercidium microphyllum*, *Olneya*, and *Prosopis* from their dominant role. The colonies of *Encelia* become less general in occurrence, except toward the Gulf, and the nearly pure stands give way to mixed shrubbery including:

Caesalpinia pumila
Acacia constricta
Coursetia glandulosa
Calliandra eriophylla
Eysenhardtia orthocarpa

(*Continued on following page*)

Phaulothamnus spinescens
Krameria parvifolia
Hyptis Emoryi
Desmanthus Covillei
Lycium exsertum
Mimosa laxiflora
Sapium biloculare
Bursera Hindsiana
Waltheria americana
Lantana horrida
Euphorbia californica
Atamisquea emarginata
Carlowrightia californica
Malpighia ovata
Forestiera neomexicana

With the gradually increasing density of shrubbery and small trees there is an almost complete elimination of the species of cacti which are abundant in the open desert to the north. *Lemaireocereus*, *Lophocereus*, and *Ferocactus Covillei* are much less frequent, colonies of *Opuntia fulgida* var. *mammillata* are still encountered, *Opuntia arbuscula* is rare, *O. Thurberi* is frequent, and *Rathbunia alamosensis* occurs in large but widely scattered thickets. On the western edge of the Plains the cacti are still prominent in the vegetation, particularly the cylindropuntias.

Southern Plains region. The southern part of the Plains of Sonora, lying south of the Río Sonora, is a narrow triangle in which there is a rapid transition from very arid plains on the west to a more broken surface and heavier vegetation on the east. In stature and density the vegetation resembles that of the western edge of the Plains north of Río Sonora, but there are a number of further additions to the dominant and subdominant species. The waning colonies of *Larrea* do not extend inland to the eastern edge of the Plains. *Encelia* is less abundant than it is to the north, but frequently reaches a height of over 2 m. *Olneya* decreases rapidly in abundance from west to east. The differentiation of the vegetation along streamways is more conspicuous than it is north of Río Sonora. In some localities the vegetation of hills is heavier than in the northern part of the Plains. On the highest mountain of the area, Sierra Libre, the desert trees and shrubs of the base are still dominant on the highest ridges, 600 m. above. The slopes of this mountain are the southernmost locality in which *Carnegiea* has been observed in abundance.

The dominant large perennials of the Plains of Sonora south of the Río Sonora are:

Olneya tesota
Cercidium floridum
Fouquieria Macdougalii
Bursera laxiflora
Jatropha cordata
Prosopis juliflora var. velutina
Ipomoea arborescens
Lemaireocereus Thurberi
Bursera microphylla
Encelia farinosa
Opuntia Thurberi
Caesalpinia pumila
Croton sonorae
Lantana horrida
Larrea tridentata
Cordia parvifolia
Pithecellobium sonorae
Jacquinia pungens
Coursetia glandulosa
Desmanthus Covillei

Several large perennials first become prominent south of the Río Sonora or do not range north of it. Among these are plants which strongly affect the physiognomy of the vegetation, although, with two exceptions, they are rarely abundant in any one spot. These include:

Forchammeria Watsoni
Ipomoea arborescens
Pachycereus pecten-aboriginum
Acacia Willardiana
Piscidia mollis
Cordia sonorae
Pithecellobium sonorae
Acacia cymbispina
Ceiba acuminata

Forchammeria, *Ipomoea*, *Piscidia*, and *Ceiba* are found on the open floor of the plains; *Acacia Willardiana* is found only on rocky slopes; *Pachycereus*, *Cordia*, *Pithecellobium*, and *Acacia cymbispina* are confined to the streamways and their bordering depressions. All these species occur here as scattered individuals, and only the two Acacias are ever sufficiently abundant and closely spaced to become the dominants of their communities. The character of these plants and their role in the vegetation are briefly described in chapter 5.

STREAMWAYS. The streamways of the Plains of Sonora are nearly all shallow. Owing to the low gradient and the abundance of sand and fine gravel in the soil, there has been very little channel cutting. Owing to the relatively heavy cover of vegetation over the general surface, the bands of much heavier vegetation along the streamways are not so conspicuous as in the more arid parts of the Sonoran Desert. Also the influence of the better moisture conditions along the arroyos here extends farther from their banks and ends gradually. Other than the Río San Miguel there are no streamways large enough to have developed extended flood plains, and there are few pure stands of large *Prosopis* such as are found along the rivers which rise outside the desert.

The most common type of vegetation along the streamways is a very irregularly spaced stand of *Prosopis*, *Cercidium floridum*, *Olneya*, *Acacia Greggii*, and *A. occidentalis*, in which the height of the trees is uneven. The stand is closed by shrubs along the larger arroyos but somewhat open along the smaller ones. Nowhere is there any consistent layering, and there are no places with continuous heavy shade and a bare floor. There are more vines in these situations than in any other desert habitat. Ephemerals and small perennials are sporadically abundant in spots with good light.

The commonest shrubs in the almost impenetrable thickets that fringe the streamways are:

Franseria ambrosioides
Acacia constricta
Lycium spp.
Condalia lycioides
Mascagnia macroptera
Anisacanthus Thurberi
Baccharis sarothroides
Aloysia ligustrina
Rathbunia alamosensis
Celtis pallida
Mimosa laxiflora
Lantana horrida
Forestiera neomexicana

Away from the streamways there are few vines in the Plains of Sonora. *Janusia gracilis* is widely distributed as either a vine or a small shrub. Several herbaceous species of *Ipomoea* are common. *Cucurbita digitata* and *C. palmata* run over the ground more often than they climb. The massive half-exposed root of *Maximowiczia sonorae* is frequently found in dry situations under low bushes, on which its stems climb during the summer rainy period.

In the thickets along streamways the vines are numerous in individuals and species. Most of them climb only to the height of the shrubs. A few with woody stems reach the tops of the trees. A nearly complete list of them follows:

Clematis Drummondii
Eupatorium sagittatum
Cardiospermum corindum
Funastrum cumanense
Commicarpus scandens
Nissolia Schottii
Sicyosperma gracile
Merremia Palmeri
Passiflora mexicana
Iresine interrupta
Cocculus diversifolius
Metastelma Watsonianum
Antigonon leptopus
Phaseolus atropurpureus
Calonyction muricatum
Matelea caudata
Marsdenia edulis

Foothills of Sonora

(Arborescent Desert. Acacia-Prosopis Region)

This subdivision of the Sonoran Desert forms the southeastern border of the continental part of that area. Much of its surface is rugged but not mountainous. Two-thirds of the Foothills area lies more than 100 km. inland from the Gulf of California. The rainfall is greater than in any of the other subdivisions, locally and perhaps exceptionally reaching 500 mm., but 70 to 80 per cent of it falls in the three summer months and there is a long period of deficient rainfall usually lasting from January or February to July. Though the vegetation of the area is distinctly desert in character, it is heavier and more continuous than in any of the other subdivisions of the Sonoran Desert.

The Foothills area is 375 km. in length from north to south, and 100 to 150 km. in width. Its northwestern corner is drained by the Río Sonora, and its central and eastern part by the Río Yaqui and its tributaries Río Moctezuma, Río Bavispe, and others. Approximately 25 per cent of the area is occupied by level or gently tilted plains, following the rivers or skirting the coast. There are innumerable hills, lava fields, and small mountains, but only three mountains rising as much as 1000 m. above the surrounding plains. The elevation of the area falls from about 1000 m. near Arizpe to sea level in the delta of Río Yaqui.

The north-and-south extent of the Foothills of Sonora is greater than that of the Plains of Sonora. The differences of 3.5° of latitude and 1000 m. of elevation between the north and south ends of the area are responsible for the conditions which underlie the principal differences of vegetation in the area.

At its northern end the Foothills area extends up the valleys of the Sonora, Moctezuma, and Bavispe Rivers. In these three projections desert vegetation is

nearly limited to the valley floor, but many species of desert plants occur above the floor on dry south slopes and in small tributary valleys. The principal valleys are separated by forested mountains. Between the Río Bavispe and the Río Moctezuma is Sierra Oputo (Sierra Moctezuma), between the Río Moctezuma and the Río Sonora is Sierra Santa Margarita, and between the Río Sonora and the Río San Miguel is Sierra Aconchi. Sierra Oputo and Sierra Aconchi have large stands of pine, and Sierra Santa Margarita is heavily forested with oaks. The region north of these mountains and north of the three projections of desert is a rolling plain covered by grassland. This is the southernmost large body of grass, of the low turf-forming type dominated by species of *Bouteloua*, that has been found west of the Sierra Madre Occidental. Each of the mountains just mentioned is flanked by a narrow and sharply dissected bajada, on which the vegetation is cleanly controlled by the topography. The undissected strips of bajada are covered with heavy stands of grass. The north slopes of the deeply cut streamways are either heavily or lightly wooded with evergreen oaks, and the south slopes are dominated by open shrubbery in which many desert plants participate.

At its southern end the Foothills of Sonora merges into thorn forest over a flat terrain which makes the transition very gradual. The southern boundary of the Sonoran Desert has been placed between the lower courses of the Río Yaqui and the Río Mayo, approximately at the place where vegetation with many open spaces occupied by xeric plants gives way to a continuous cover of summergreen trees. There are, however, a few small areas as far south as the Río Fuerte in which the vegetation has the open desert aspect, heightened by an abundance of *Cercidium* and *Opuntia*.

The delta of the Río Yaqui lies mainly south of the present lower and westward course of the river. Much of this extensive area is now in cultivation and produces important crops of wheat, rice, and garbanzo. The original vegetation of the delta is stated to have been like that of the parts which remain uncultivated, a closed or open forest of *Prosopis juliflora* var. *Torreyana* with heavy shrubbery and a very rich representation of cacti (pl. 19). Near the coast there are very few trees, and the areas of dense shrubbery are interrupted by lagoons and small areas of dunes.

The Foothills area occupies an important position in the vegetation of Mexico. On the north it is bounded by a temperate type of grassland, and on the south by arid subtropical thorn forest. On the west it is sharply limited by the level, arid coastal plain, and on the east by the lower slopes of the outlying ranges of the Sierra Madre Occidental, where an increase of rainfall is immediately encountered.

Though the Foothills of Sonora is not a mountainous area, it is sufficiently rugged to present a large variety of habitats. A few of the dominant plants of the Sonoran Desert are more abundant in it than elsewhere, but the majority of them are commoner in adjacent areas and are restricted to the Foothills habitats which most nearly resemble their areas of greatest abundance. The thorn forest

has contributed heavily to the flora of the Foothills of Sonora, and many of these plants are conspicuous in the vegetation of the southern half of the area. The great majority of plants which range north from Guerrero and Jalisco as far as latitude 29° to 30° N. reach their northern limit in the Foothills of Sonora and are absent from the same latitude in the Plains of Sonora and the Central Gulf Coast.

Northern Foothills region. The area north of the latitude of Ures is largely comprised in the three nearly parallel valleys of the Sonora, Moctezuma, and Bavispe Rivers. All these rivers carry a heavy summer discharge, which has restricted the formation of flood plains. Their courses frequently run alongside the hills for many kilometers. There are rolling plains surrounding Moctezuma and Ures, and narrow stretches of valley floor at many localities farther north.

Between Cumpas and Moctezuma there is a broad valley in which the vegetation is very open, forming a 20 per cent cover. The dominant plants are widely spaced small trees of *Prosopis juliflora* var. *velutina* and an open stand of *Encelia farinosa*. The principal elements of the vegetation in this valley are:

***Prosopis juliflora var. velutina
***Encelia farinosa
**Cercidium sonorae
**Fouquieria splendens
**Dodonaea viscosa var. angustifolia
**Lemaireocereus Thurberi
**Celtis pallida
*Mimosa laxiflora
*Opuntia fulgida
*Opuntia Thurberi
*Opuntia Engelmannii
Condalia spathulata
Karwinskia Humboldtiana
Forestiera neomexicana
Janusia gracilis

The physiognomy of this area, and similar ones in the adjacent valleys, suggests the Arizona Upland, but the vegetation does not include *Larrea tridentata*, *Cercidium microphyllum*, *C. floridum*, *Carnegiea gigantea*, and *Olneya tesota*. Neither does it include any of the species which are common in the thorn forest.

The elevation of the three valleys is between 500 and 800 m. All of them have extensive drainage areas lying in grassland plains or forested mountain slopes, and all are subject to pronounced inversion of temperature. No adequate temperature data are available for this area, but the topographic situation is identical with that of localities which have been investigated in Arizona (Shreve, 1912; Turnage and Hinckley, 1938). By reason of air drainage from large elevated areas, the inversion of temperature probably results in absolute winter minima in these valleys from 15° to 20° F. lower than the minima on the adjacent bajadas and slopes 50 to 100 m. above. Freezing temperatures occur nearly every winter at Cumpas, Moctezuma, and Ures, but the maximum duration of temperatures below 32° F. is not known.

*Here and below, asterisks indicate relative abundance: three asterisks, greatest abundance, etc.

The behavior of a number of large perennials of southern Sonora which have been under cultivation at Tucson (including *Ceiba acuminata*, *Bursera microphylla*, *B. laxiflora*, *Jatropha cordata*, *Piscidia mollis*, *Pithecellobium sonorae*) has shown that they are killed to the ground by the minimum temperature and frost duration of a normal winter. Winter temperature conditions appear, therefore, to be responsible for the absence of some of the characteristic plants of southern Sonora from the valley floors of the northern Foothills of Sonora.

North of Baviacora, Cumpas, and Granados, the south slopes above the influence of temperature inversion afford a safe habitat for plants of southern range which are absent from the valleys. The observations of the author and the collections made by Stephen S. White in the area immediately outside the Sonoran Desert indicate the occurrence of a number of Sonoran Desert plants in warm situations which are well above their distributional limits in the valleys. The following plants have been found at the localities indicated:

Ceiba acuminata Bursera laxiflora Lysiloma divaricata Parthenium Stramonium Sapium biloculare Ficus petiolaris	Cañon Higuera, west of Moctezuma
Sapium biloculare	Bajada above Baviacora
Fouquieria Macdougalii	Several localities above Granados
Diphysa Thurberi	Cañon de Huepari, north of Aribabi
Acacia cymbispina	Puerto de Huepari, north of Aribabi
Ipomoea arborescens Jatropha cordata	Aguaje de Bacatejaca, between Granados and Bacadehuachi
Manihot angustiloba	Bajada of Sierra Santa Margarita, west of Cumpas
Manihot angustiloba	Cañon Bavispe
Erythrina flabelliformis	Río Bonito

The bajadas and rolling plains lying just above the valley floor of the Río Moctezuma are covered by trees and shrubs with a density which varies from a 20 per cent to a 60 per cent cover. Perennial grasses are here more abundant than in any other part of the Sonoran Desert. As one ascends the bajadas the trees and shrubs become fewer and the patches of grass more continuous. At an elevation of 800 m. the aspect of the vegetation is that of grassland, with an open sod of *Bouteloua radicosa* and *B. eludens* and widely scattered trees of *Prosopis juliflora* var. *velutina* and *Acacia Farnesiana*.

The characteristic perennials of the upper areas of desert in the Sonora, Moctezuma, and Bavispe valleys are listed below. In order to indicate the strong relationship between the northern part of the Foothills of Sonora and the Arizona Upland, the initials of the latter area have been placed after the names of the plants which are common to the two.

Prosopis juliflora var. velutina (AU)
Acacia cymbispina
Fouquieria splendens (AU)
Celtis pallida (AU)
Acacia Greggii (AU)
Cercidium sonorae
Fouquieria Macdougalii
Randia Thurberi
Condalia spathulata (AU)
Jatropha cardiophylla (AU)
Bursera filicifolia
Lemaireocereus Thurberi
Encelia farinosa (AU)
Karwinskia Humboldtiana
Caesalpinia pumila
Eysenhardtia orthocarpa
Opuntia Thurberi
Bursera laxiflora

In the upper levels of the Foothills of Sonora there are many herbaceous perennials and small woody perennials which do much to heighten the aspect of density during the summer months, when they are in leaf and in flower. Many of these plants are confined to the light shade of *Prosopis* or *Acacia* or are found on banks along arroyos. The principal species are:

Turnera diffusa
Franseria ambrosioides
Ruellia nudiflora
Elytraria imbricata
Abutilon sonorae
Brickellia Coulteri
Hintonia latiflora
Phaseolus atropurpureus
Antigonon leptopus
Ayenia pusilla
Carlowrightia californica
Commicarpus scandens
Talinum paniculatum
Desmodium cinerascens
Salvia Seemannii
Rivina humilis
Brongniartia Palmeri

Central Foothills region. The region between Ures and Tecoripa is one of low relief in which the surface is about equally divided between hills or volcanic mesas and plains or slopes of low gradient. It is here that trees become an important feature of the desert vegetation to an extent that is matched in the north only in the most favorable situations of the Arizona Upland. The dominant arborescent forms are small leguminous trees with winter-deciduous compound leaves and leaflets rarely exceeding 20 sq. mm. in area. The crown is flat, and the form of all the trees in a community is remarkably uniform. The height varies from 4 to 12 m. according to the site. Local distribution of the leguminous trees is determined by soil moisture, and there is great variation in the density of the stands. Low situations often support stands in which the crowns meet, whereas in the higher situations the trees stand well apart, often separated by distances of 50 to 75 m. The most abundant trees are *Prosopis juliflora* var. *velutina* and *Acacia cymbispina*. In low situations and along arroyos *Lysiloma divaricata*, *L. Watsoni*, and *Pithecellobium mexicanum* are characteristic. In the western half of the area, *Olneya tesota* is frequent in the driest situations.

On rocky slopes and hillsides the leguminous trees are absent or infrequent. Here the dominant arborescent forms are *Bursera odorata*, *B. laxiflora*, and *Jatropha cordata*, accompanied by a small percentage of other trees and by *Pachycereus pecten-aboriginum* and *Fouquieria Macdougalii*.

In the central Foothills region there are many short valleys or embayments of structural origin into which there is no surface drainage. These occur around the volcanic mesas and also along the major and minor streamways. The bottom of the embayments has an accumulation of soil in which the moisture content is relatively high, and the absence of cold-air drainage from a large or elevated region makes them warm. In such situations along the Río Moctezuma north of its confluence with the Río Bavispe are found the northernmost examples of *Acacia cymbispina*, the palm *Erythea Roezlii*, and the woody composite *Parthenium Stramonium*.

In a few localities in this area above an elevation of 750 m. the upper limit of desert is indicated by the abundance of coarse perennial bunch grasses and the occurrence of open groves of *Quercus chihuahuensis*.

Trees are abundant and ubiquitous in the arborescent desert of the Foothills of Sonora, but shrubs also play an important part in the vegetation. In the most favorable situations, occupied by dense stands of *Acacia* or *Lysiloma*, shrubs are few and the floor is clean (pl. 34). Elsewhere shrubs are abundant, growing in scattered groups in the open, massed under the trees, or forming thickets so dense that they can be penetrated only by following a devious route. In the largest level areas the shrubs are as widely spaced as the trees. Immediately south and southeast of Ures there are extensive plains drained by the Río Sonora. In them there is considerable diversity of substratum, comprising deep granitic soils, shallow volcanic clay and loam, and aggraded limestone areas with no soil other than that which fills the depressions in the rock surface. In this area the distribution of the vegetation is very irregular and its aspect changes radically from place to place.

Several of the dominant plants of the Arizona Upland and the Plains of Sonora are found in the most arid situations along the western edge of the Foothills of Sonora, but all of them are rare or absent along the Yaqui River. These plants include *Cercidium microphyllum*, *C. floridum*, *Carnegiea gigantea*, *Encelia farinosa*, *Acacia Greggii*, and *Lemaireocereus Thurberi*. *Celtis pallida* is infrequent in the central Foothills area, but extends far into the mountains east of the Sonoran Desert. *Olneya* is locally abundant in the western half of the Foothills area, but is nowhere dominant or subdominant. The desert aspect of vegetation and the plants characteristic of the most arid parts of the Sonoran Desert are found chiefly in the part of the Foothills of Sonora which lies north of Tecoripa and west of the Río Yaqui.

The following list of the characteristic large perennials of the plains and bajadas of the central Foothills of Sonora is based on determinations of composition in twelve localities in the leguminous type of arborescent desert:

***Prosopis juliflora var. velutina
***Acacia cymbispina
***Cercidium sonorae
***Haematoxylon brasiletto
***Caesalpinia pumila
***Karwinskia Humboldtiana
**Lysiloma divaricata
**Acacia pennatula
**Opuntia Thurberi
**Cercidium floridum

**Opuntia fulgida
**Croton sonorae
**Lantana Camara
*Olneya tesota
*Lysiloma Watsoni
*Pithecellobium mexicanum
*Jatropha cardiophylla
*Guazuma ulmifolia
*Randia Thurberi
*Sapium biloculare
*Ipomoea arborescens
*Encelia farinosa
*Eysenhardtia orthocarpa
*Pachycereus pecten-aboriginum
*Acacia Farnesiana
Piscidia mollis
Acacia Greggii
Ceiba acuminata
Jacquinia pungens
Guaiacum Coulteri
Schaefferia Shrevei
Caesalpinia pulcherrima
Dodonaea viscosa
Randia laevigata
Celtis pallida
Erythea Roezlii
Nolina matapensis
Bursera odorata

In the central Foothills of Sonora may be noted the almost universal difference in physiognomy and composition between the vegetation of granitic slopes and that of volcanic eruptives. The difference manifests itself in this area by greater irregularity in the emplacement of large plants on granite, frequent changes of dominance, a heavier stand of shrubs, and a greater amount of grass. The eruptives have a simpler total composition, a smaller number of dominants more uniformly distributed, fewer shrubs, and very few grasses.

The granite mountains in the vicinity of Ures have a basal elevation of about 500 m., and their vegetation is desert up to about 1000 m. In the following list are noted the common plants of the lower slopes of these mountains, with indication of their relative abundance. Many other infrequent or scatteringly distributed plants add to the density and variety of the vegetation.

***Cercidium microphyllum
***Fouquieria Macdougalii
**Ipomoea arborescens
**Prosopis juliflora var. velutina
**Cercidium sonorae
**Jatropha cordata
**Franseria cordifolia
**Karwinskia Humboldtiana
**Mimosa laxiflora
**Lemaireocereus Thurberi
**Lantana Camara
*Guaiacum Coulteri
*Ceiba acuminata
*Piscidia mollis
*Lysiloma divaricata
*Cassia biflora
*Encelia farinosa
Erythrina flabelliformis
Opuntia Thurberi
Tecoma stans
Jatropha cardiophylla
Diphysa suberosa
Agave yaquiana
Randia laevigata

The volcanic hills and mesas of the central Foothills of Sonora lie between elevations of 300 and 600 m. On the gentle slopes well provided with soil are found the most uniform stands of *Bursera odorata* and *Jatropha cordata*, growing in stands so open that the crowns of the trees are separated by a distance of one to three times their diameter. The accompanying shrubs are also widely spaced.

The mesas are bordered by sharp but well weathered escarpments. At the base

of an escarpment and on its talus the vegetation is relatively dense. The two dominant trees of the gentle slopes are joined by *Ipomoea arborescens*, *Pachycereus pecten-aboriginum*, *Acacia cymbispina*, *Cercidium sonorae*, *Acacia pennatula*, and a number of shrubs, as enumerated below.

The lava fields which form the level surface of the mesas are often more poorly provided with soil than the fields which lie at an accordant level with the surrounding area (as described on pp. 56–57). The vegetation of the mesas is very similar in composition to that of the gentle slopes, but the plants are smaller and more widely and unevenly spaced.

The tops of the volcanic mesas give every indication of providing a poorer water supply than any other habitat in the Foothills region. During the period of very low precipitation from February to June, the moisture supply sinks to a level which prevents all vegetative activity. It is of interest that none of the cacti and few of the nonsucculent plants of the Lower Colorado Valley and the Arizona Upland are found on the arid mesas. None of the strictly evergreen woody plants of neighboring habitats are found, except the partly deciduous *Sapium biloculare* and *Dodonaea viscosa*. Cacti are sparingly represented by a few thorn forest species, including *Pachycereus pecten-aboriginum*, *Opuntia fuliginosa*, and *O. tomentosa*. *Olneya* and *Cercidium microphyllum* are infrequent.

Throughout the Foothills of Sonora the arid aspect of the landscape in winter and spring is relieved only by the appearance of leaves in March on individuals of *Prosopis*, *Lysiloma*, and *Pithecellobium* which are growing where there is a good soil-moisture supply. With the beginning of the summer rains there is a rapid development of foliage by the trees and shrubs and an equally prompt appearance of root perennials and ephemerals. The lush and verdant aspect of the landscape persists until the latter part of September or often to the middle of October. The approach of the dry autumn is first indicated when the leaves of *Jatropha* turn yellow and those of *Bursera* and *Haematoxylon* turn red. At that season the colorful landscape accurately reveals the abundance of these plants and the pattern of their distribution.

The following are the characteristic plants of the volcanic slopes and mesas:

***Bursera odorata
***Jatropha cordata
**Cercidium sonorae
**Fouquieria Macdougalii
**Haematoxylon brasiletto
**Ipomoea arborescens
**Croton sonorae
*Randia Thurberi
*Sapium biloculare
*Acacia pennatula
*Opuntia Thurberi
*Krameria paucifolia
*Caesalpinia pumila
*Opuntia fuliginosa
Abutilon Pringlei
Ceiba acuminata
Dodonaea viscosa
Guazuma ulmifolia

Lava beds. At a number of localities in the central Foothills of Sonora there are lava beds several square kilometers in area. The surface of the beds is nearly level and extremely rough, but affords many crevices and pockets of fine clay. One of

the largest fields evidently originated by extrusive activity of a small cone 32 km. south-southeast of Moctezuma. From this the lava flowed southwest and spread to a width of about 15 km. along the left bank of the Río Moctezuma, its southern edge being just above Batuc.

The lava beds may be clearly distinguished at a distance by the exposed dark brown basalt and by their heavy cover of vegetation, the color tone of which is a much darker green than that of the surrounding vegetation. There is much bare rock in the lava fields, but plants occupy all the crevices and patches of soil very densely and there are many heavily covered areas of nearly a hectare. As was brought out in connection with the lava beds of the Lower Colorado Valley, the soil-moisture conditions in such a habitat are more favorable than on a deep, homogeneous soil. The character of the surface prevents the formation of drainage systems, and there is almost no runoff. Infiltration along the rock surfaces is good, the fine clay is highly retentive, and evaporation is reduced by partial shading and by the interruption to wind action due to protruding masses of rock. Among the plants characteristic of the lava beds are several which are north of their normal limits. Several considerations indicate that the lava beds are a warmer habitat than the bajadas or plains surrounding them.

Shrubs predominate over trees on the lava beds, but there is no constant relation between the abundances of the two. The profile of the vegetation is very irregular. The following list of characteristic plants is drawn from the examination of several localities in the field near Batuc:

Cercidium sonorae
Ipomoea arborescens
Fouquieria Macdougalii
Opuntia fuliginosa (tall platyopuntia)
Croton sonorae (shrub, 1–2 m.)
Eysenhardtia orthocarpa
Mimosa laxiflora
Esenbeckia Hartmanii (southern)
Randia obcordata (slender tree, 3–5 m.; southern)
Franseria cordifolia (suffrutescent perennial, 1–1.5 m.)
Guaiacum Coulteri (compact tree, 3–4 m.)
Jatropha cardiophylla
Acacia cymbispina (tree, 5–6 m.; southern)

Annuals and herbaceous perennials are very abundant in the shade of trees and rocks in the late summer. Perennial grasses are infrequent, but annual species are common in open situations.

Southern Foothills region. This area comprises the region south of the latitude of Tecoripa and is the southernmost part of the Sonoran Desert on the mainland of Mexico. On the west and north of the Río Yaqui the central feature of the topography is Sierra Bacatete, which rises above the level of desert vegetation and is surrounded by low hills and coastal or fluviatile plains. To the east and south of the Río Yaqui an area of about 1800 sq. km. is occupied by the delta, which has its apex near Cajeme (Ciudad Obregón). South of Cajeme the coastal plain extends inland for 30 to 40 km. North of Quiriego the inner edge of the Foothills of Sonora is a region of low, close-set hills.

In the southern Foothills the prevailing vegetation still exhibits the charac-

teristics of desert, at the same time that 20 to 30 per cent of the area is occupied by littoral or thorn forest vegetation. The littoral communities include the strand, small sand dunes, mangrove swamps, marshes, and saline flats as well as low thickets of shrubbery and open forests of *Prosopis juliflora* var. *Torreyana*. Thorn forest is found along streamways and on flood plains and valley bottoms. The relatively dense thorn forest vegetation almost invariably terminates sharply at a variable distance from a streamway. Beyond these edges are open stands of desert plants.

The hills of the southern Foothills of Sonora are more heavily clothed with trees and tall shrubs than are those of the central Foothills. The coverage is from 75 to 90 per cent. The single canopy of xeric trees has an irregular height of 4 to 10 m. The commonest shrubs range in height from 0.5 to 6 m. Microphyllous trees are dominant, most of them being Leguminosae, but the number of broad-leaved trees is here greater than in any type of vegetation previously described. Three species of large cacti are abundant and others are frequent. *Agave* is uncommon except on rock outcrops.

In this habitat all the criteria of desert, constantly exemplified in the areas to the north, have become so weakly expressed that much of the hill vegetation in the southern Foothills area is more closely allied to thorn forest than it is to desert. The percentage of cover is high, the stature of the plants is consistently greater, and the diversity of life forms is very much less than in the desert. The denser cover results in a controlled runoff and a considerable accumulation of plant litter. Though the surface of the slopes is stony, the soil is several decimeters deep, except in the steepest places, and there is a clear differentiation of soil and subsoil. The margins of streamways are more strongly held in place by the vegetation than is the case in the desert, and the influence of the better moisture conditions of streamways extends farther from the bed of the stream.

The open desert communities which occupy the upland of the southern Foothills of Sonora are dominated by an irregularly spaced stand of trees with scattered shrubs and widely spaced cacti. The coverage may be as low as 40 per cent or as high as 70 per cent. These areas may be readily traversed in any direction, which is not true of the dense growth in the bands of thorn forest. Approximately half the stand of trees is made up of the first 6 species indicated in the following list as being of the first order of abundance. The remainder of the arborescent vegetation is made up of a much larger number of trees, either consistently or sporadically distributed. The most conspicuous cactus is *Lemaireocereus Thurberi*, but the most common one is *Opuntia fulgida* var. *mammillata*, which occurs frequently, sometimes in colonies, rarely exceeds 1 m. in height, and is very sparing in the formation of flowers and fruit.

The characteristic plants of the desert upland of the southern Foothills of Sonora are as follows:

***Prosopis juliflora var. velutina (tree)
***Cercidium floridum (tree)
***Acacia cymbispina (tree)
***Fouquieria Macdougalii (tree)
***Cercidium sonorae (tree)
***Piscidia mollis (tree)

***Eysenhardtia orthocarpa (shrub)
***Karwinskia Humboldtiana (shrub)
***Guazuma ulmifolia (shrub)
**Bursera microphylla (tree)
**Jatropha cinerea
**Opuntia fulgida var. mammillata
**Pithecellobium sonorae
**Bursera laxiflora
**Guaiacum Coulteri
**Lemaireocereus Thurberi
**Janusia gracilis
*Condalia lycioides
*Haematoxylon brasiletto
*Lycium Berlandieri var. peninsulare
*Mimosa laxiflora
Krameria sonorae
Ceiba acuminata
Cassia biflora
Turnera diffusa
Ruellia californica
Fouquieria peninsularis
Desmanthus Covillei
Euphorbia colletioides
Citharexylum flabellifolium
Hyptis Emoryi

Mention has been made of the grouping of herbaceous ephemerals and young perennials in the shade of large perennials, which is common in all but the driest parts of the Sonoran Desert. In the Plains of Sonora and the Foothills of Sonora this feature is constant and clearly marked, and the number of root perennials and young trees and shrubs is greater than the number of ephemerals. These groups of subordinate plants themselves do much to improve the soil-moisture conditions during the summer rains, and the groups very commonly come to extend well beyond the shade of the sheltering trees. Where closely spaced trees are all surrounded by small plants, the groups coalesce into a single area, often 50 m. in diameter. The edge of a group is almost invariably well defined, the coverage dropping from 100 per cent in it to 30 to 40 per cent outside it.

In the subordinate groups are found young plants of the large desert perennials and desert shrubs, many young or small plants characteristic of the bands of thorn forest, and a large number of root perennials and ephemerals which do not occur in the open. Several trees which are abundant in thorn forest and infrequent in desert (*Ipomoea arborescens*, *Ceiba acuminata*, *Cordia sonorae*, *Pithecellobium sonorae*) doubtless owe their desert occurrence to conditions favorable for their germination and early growth in subordinate groups which no longer exist.

A very obvious phase of the transition from desert to thorn forest may be observed in connection with the types of habitats in which the two vegetations occur near their meeting ground. North of Cajeme the outlying bodies of thorn forest occupy the most favorable habitats in a predominantly desert vegetation. South of Cajeme small areas of desert vegetation are found in the driest situations of the prevailing thorn forest.

The bands of thorn forest which follow the flood plains of rivers and the margins of smaller streams are conspicuous by their density and the occurrence of trees more than 8 to 10 m. in height. On account of the irregularity of the canopy and the thin shade of the microphyllous trees, the vegetation shows no layering. There is usually a solid body of foliage from the ground to the treetops. The regular canopy of pure stands of *Acacia cymbispina* here serves merely to form a general level with which a few other trees are accordant and several are not.

Among the latter are the broad-leaved trees *Ipomoea arborescens*, *Sapindus Saponaria*, *Vitex mollis*, and *Cordia sonorae*, all of which occur farther north, and *Cassia emarginata*, *Zizyphus sonorensis*, and *Albizzia sinaloensis*, here at their northern limit. These are the trees which often exceed 10 m. in height (except *Vitex* and *Zizyphus*).

The dense undergrowth of shrubs is commonly dominated by *Franseria cordifolia*, which is from 6 to 10 dm. high and is not accompanied by lower herbaceous perennials. In other situations a low carpet of small perennials covers the ground.

The following list embraces the most generally observed plants found along streamways in the southernmost part of the desert. The broad-leaved trees are indicated by "B."

***Acacia cymbispina
***Franseria cordifolia
**Ipomoea arborescens (B)
**Pithecellobium sonorae
**Cassia emarginata (B)
*Coursetia glandulosa
*Zizyphus sonorensis (B)
*Rathbunia alamosensis
*Cordia sonorae (B)
*Randia echinocarpa (B)
*Sapindus Saponaria (B)
*Celtis pallida
*Pachycereus pecten-aboriginum
*Franseria ambrosioides
*Lantana Camara
*Acacia occidentalis
*Opuntia Thurberi
*Lagascea decipiens
*Lantana velutina
*Brickellia Coulteri
*Plumbago scandens
Vallesia glabra (B)
Alvaradoa amorphoides
Jacquinia pungens
Bumelia occidentalis (B)
Jacobinia ovata (B)
Caesalpinia pulcherrima
Vitex mollis (B)
Opuntia fuliginosa
Cardiospermum corindum
Albizzia sinaloensis (B)
Colubrina glabra
Caesalpinia platyloba (B)
Celosia nitida
Pereskiopsis Porteri
Gouania mexicana
Chiococca petrina
Parthenium Stramonium (B)
Xanthoxylum sonorense
Solanum amazonium (B)
Hintonia latiflora
Plumeria acutifolia (B)

The ecological features of the undisturbed parts of the delta of the Río Yaqui are very complex and have not been examined in detail. Mangrove swamp occupies a few small areas on the coast. *Rhizophora Mangle* is the dominant tree, accompanied by *Avicennia nitida* and *Conocarpus erecta*. *Rhizophora* occurs infrequently around Guaymas and as far north as Tiburón Island, but does not develop its characteristic stands. Small dunes skirt the coast just inside the upper beach. Their total area is very small.

The large level expanse of light gray alluvial soil which covers the delta shows great variety in its local plant communities. Along the coastal edge there is much bare ground and the prevailing plants are halophytic shrubs, including *Atriplex canescens*, *Suaeda fruticosa*, *Lycium carinatum*, *Maytenus phyllanthoides*, *Stegnosperma halimifolium*, *Phaulothamnus spinescens*, and *Lippia Palmeri*. Farther

inland the shrubbery becomes denser and taller, and *Prosopis juliflora* var. *Torreyana* more frequent. In its original condition the delta area must have included many heavy stands of *Prosopis*, but there are none now which compare with the groves along the Altar and Magdalena Rivers.

Almost throughout the northern edge of the delta there is a strong representation of cacti in the vegetation (pl. 19). The most abundant are *Lemaireocereus Thurberi* and *Opuntia fulgida* var. *mammillata*. *Rathbunia alamosensis* is very frequent, and *Pachycereus pecten-aboriginum* and *Ferocactus* sp. are often seen. In some localities *Mammillaria Swinglei* is remarkably abundant. The substratum for the cacti is a heavy alluvial clay, which appears to be ill suited in texture and aeration for such rich stands of succulent plants.

Central Gulf Coast

(Sarcocaulescent Desert. Bursera-Jatropha Region)

The part of the Sonoran Desert designated as the Central Gulf Coast lies along the shores of the Gulf of California and is partly in Sonora and partly in Baja California. The Sonoran part of the area extends from the southern end of the dunes and sandy plains of the Lower Colorado Valley to the delta of the Río Yaqui. In Baja California the area extends from Bahía Los Angeles to the vicinity of Cerralvo Island, just south of La Paz. The largest islands in the Gulf, Angel de la Guarda and Tiburón, as well as the numerous smaller islands, are also a part of the area. In Sonora the vegetation of the Central Gulf Coast extends inland for 20 to 30 km. and merges gradually into that of the Lower Colorado Valley or the Plains of Sonora. In Baja California it extends inland for a shorter and variable distance, being bounded by the drainage divide of the peninsula or by the chains of hills lying nearest the coast.

The Central Gulf Coast has been examined at five localities in Sonora and six in Baja California, involving stretches of 30 to 100 km. in each locality. Comparison of these areas shows that there is essential identity in the vegetation on the two sides of the Gulf. Several important dominants of Baja California are very local in their occurrence in Sonora and a few are absent, so far as known. A very small number of large perennials are found in the Sonoran section which are absent from Baja California. In the physiognomy of the vegetation there are no constant differences to distinguish the two coasts. In several cases, to be mentioned later, the same place is taken in the vegetation of the two coasts by different but closely related species. North of the Central Gulf Coast area the flora on the two sides of the Gulf is nearly identical.

The Gulf coast is occupied in part by hills and small mountains rising abruptly from the beach and in part by bajadas extending far inland. The most mountainous section of the Sonoran coast extends for 80 km. north from Guaymas. In Baja California the coast is prevailingly rugged almost throughout its length. There are several broad bajadas between Bahía Los Angeles and the Tres Vírgenes peak, but only narrow wedges of outwash material south of that. South of Bahía

Concepción the Central Gulf Coast area is confined to a narrow strip along the base of Sierra de la Giganta.

The soils which support the vegetation of this subdivision are shallow, coarse, and covered with rock fragments. Only where streamways debouch to the Gulf are there areas of boulder-filled sand. Dunes are infrequent and small. Lagoons, marshes, and mangrove swamps are few and small except at several localities in Bahía Concepción. The drainageways of the area are all small and rarely in flood. The Río Sonora is the only large stream which originates inland and cuts across the Central Gulf Coast. At the head of Bahía Concepción there is no evidence that any drainage other than sheet floods ever enters the bay.

The few climatic records available for the Central Gulf Coast, together with the evidence of the vegetation, indicate that it is the driest subdivision of the Sonoran Desert. In Baja California, the annual mean for Santa Rosalía is 138 mm. and for Mulegé 105 mm. In Sonora, the mean for Guaymas is 263 mm. The winter rains of the Pacific coast of Baja California rarely extend inland beyond the mountainous axis of the peninsula, and are exceeded by the winter rains on the coast of Sonora. The rains which sporadically visit the Central Gulf Coast in Baja California result from the northward extension of the storms which commonly visit the mountains of the Cape Region in the summer months.

The vegetation of the Central Gulf Coast exhibits its lowest and most open phase and its most simple composition within 5 km. of the beach at the lower ends of the long bajadas which descend from the interior. Hills and rocky slopes near the strand are also thinly covered with shrubs and small individuals of the large perennials (pl. 20). The margins of streamways and their broad, sandy beds are occupied by scattered stands of *Baccharis*, *Hymenoclea*, *Franseria ambrosioides*, and *Chilopsis*. On both bajadas and hills there is a slight increase in density and a gradual increase in number of species from coast to interior, reaching a stable maximum about 12 to 14 km. inland.

In spite of the similarity of the vegetation on the coasts of Sonora and Baja California, there is nevertheless sufficient difference to warrant separate description of the two.

Gulf coast of Sonora. The transition from the dunes and sandy plains of the Lower Colorado Valley to a hard surface takes place on the Sonoran coast a short distance above Puerto Lobos, which is 45 km. north of Libertad. In this vicinity *Larrea* and *Franseria dumosa* begin to yield their dominance to a group of large perennials in which *Larrea* is uncommon in pure stands and *Franseria fl* only locally abundant. The new group of dominants includes *Cercidium* sio*ridum*, *Olneya tesota*, *Bursera microphylla*, *Jatropha cinerea*, *J. cuneata*, *Opuntia Bigelovii*, and *Fouquieria splendens*. On all the plains and bajadas more than 5 km. from the beach, some or all of these plants form the matrix of the vegetation. In the driest situations there are few shrubs, but their numbers greatly increase along streamways, in depressions, and at the base of hills. Shrubs are found almost exclusively in the open and not closely assembled under the trees. No

shrub or root perennial has been noted in this region which occurs only in the shade of large plants, except the vine *Brandegea*.

The belt of vegetation along the immediate coast is low, very open, without trees, and monotonous in its aspect. The coverage rarely exceeds 15 to 20 per cent. The dominant plant is *Frankenia Palmeri*, a microphyllous gray shrub 4 to 8 dm. in height. Within reach of salt spray *Frankenia* and *Atriplex canescens* are commonly the only plants. Farther from the beach other plants appear, and there is a rapid transformation for a distance of 3 to 5 km. *Frankenia* rarely occurs as much as 3 km. inland. The plants which characterize the extreme coastal belt are:

Frankenia Palmeri
Atriplex canescens
Lycium Fremontii
Suaeda ramosissima
Euphorbia misera
Encelia farinosa
Stegnosperma halimifolium
Jatropha cuneata
Franseria dumosa
Errazurizia megacarpa

On the bajadas which extend far inland, *Frankenia*, *Suaeda*, *Euphorbia*, and *Stegnosperma* are not found beyond the vicinity of the beach. The vegetation beyond their range is made up of the following species:

Cercidium floridum
Prosopis juliflora var. Torreyana
Fouquieria splendens
Jatropha cuneata
Bursera microphylla
Olneya tesota
Pachycereus Pringlei
Bursera Hindsiana
Encelia farinosa
Larrea tridentata
Solanum Hindsianum
Acacia constricta
Horsfordia alata
Jatropha cinerea
Hyptis Emoryi
Sapium biloculare
Opuntia Gosseliniana
Acacia Greggii
Simmondsia chinensis
Cordia parvifolia
Atamisquea emarginata
Mimosa laxiflora
Ferocactus acanthodes

On the coast 10 km. south of Libertad is the only colony of *Idria columnaris* known on the mainland. The trees occupy the north slope of a low granite ridge which runs east from the beach, and follow the ridge inland for about 3 km. There are none on the south slope of the ridge, and none have been found elsewhere in the vicinity or anywhere else in Sonora. The total number of individuals is probably about 2000. Reproduction is good, and the tallest individuals are 12 to 14 m. high, as compared with the highest known trees, 22 m. *Idria* is very abundant throughout the central third of Baja California, and its occurrence at a single locality in Sonora is probably due to a chance natural introduction rather than to survival from a former wider occurrence.

There is little change in the vegetation southward along the coast. The region opposite Tiburón Island and the island itself closely resemble the vicinity of Libertad. *Cercidium*, *Olneya*, *Bursera*, *Fouquieria*, and *Jatropha* dominate the

hills in very open stands of small trees. *Lemaireocereus* and *Opuntia Bigelovii* are the most common cacti. *Pachycereus Pringlei* is abundant, but only on nearly level ground, whether hard or sandy.

The largest streamways are bordered by *Prosopis juliflora* var. *Torreyana*, *Olneya tesota*, *Acacia Greggii*, and *Bursera Hindsiana*. The margins of broad, sandy arroyos are occupied by light or heavy stands of the shrubs *Hymenoclea pentalepis*, *Baccharis Emoryi*, *Franseria ambrosioides*, *Hyptis Emoryi*, *Haplopappus sonoriensis*, *Beloperone californica*, *Bebbia juncea*, and *Lagascea decipiens*.

Tiburón Island and the neighboring coast are of interest as being the southernmost locality in Sonora for *Koeberlinia spinosa*, *Franseria deltoidea*, *Simmondsia chinensis*, *Ferocactus acanthodes*, *Opuntia arbuscula*, and *Atriplex polycarpa*, as well as the northern limit for *Rhizophora Mangle*, *Colubrina glabra*, *Lippia Palmeri*, *Maytenus phyllanthoides*, *Acacia Willardiana*, and *Viscainoa geniculata*. *Viscainoa*, like *Idria*, is abundant in Baja California, but is now known in Sonora only at three stations between Tiburón Island and Guaymas.

For 60 km. south of the mouth of the Río Sonora the Gulf is bordered by the low, featureless Llano de San Juan Bautista, which gives some evidence of deltaic origin. The vegetation of this plain, so far as it has been explored, is a very open stand of *Olneya tesota*, *Cercidium floridum*, and *Bursera microphylla*, with scattered thin stands of *Larrea*. The drainageways fall at a very low gradient and are choked with sand. Sudden changes in the course of the drainage frequently occur, flooding open areas and stopping the water supply of large colonies of *Cercidium* and *Olneya*. Open groves of trees killed in this way are common. The extremely hard heartwood of *Olneya* resists decay and termites for many years. After the death of a tree, the sapwood around the base is soon etched away by the sand which blows along the surface of the ground, but the heartwood is much more resistant and long supports the skeleton of the tree.

From the southern edge of the Llano de San Juan Bautista at the Estero de Tastiota, southward to Guaymas, a distance of 80 km., low mountains rise almost continuously directly from the shore. This section of the coast is difficult of access from the interior and has few suitable places for landing from a boat. The vegetation is poorly known except at the southern end in Bahía San Carlos and in the vicinity of Guaymas. General impressions of this coast have been obtained in skirting it closely by boat along a stretch of 20 km. north of Bahía San Carlos.

The vegetation of this region is open and very xeric except on some of the steep slopes which face immediately on the Gulf. These slopes are well covered by shrubs, which are in leaf from March to November, even in seasons when the plants 2 or 3 km. inland are leafless. Where gentle slopes face the Gulf, the vegetation is low and open, rarely presenting a green appearance. Where the floor of a large valley opens to the Gulf, there is a band of heavier vegetation, which retains a green appearance after the rainy seasons for one or two months longer than the interior plains.

In the vicinity of Guaymas the vegetation of both hills and plains is richer in

composition than it is in similar habitats near Tiburón Island. A few level areas with deep soil are occupied by nearly pure stands of *Larrea* or of *Prosopis juliflora* var. *articulata*. The prevailing shallow soils and hillsides are clothed with the following perennials:

***Bursera microphylla
***Prosopis juliflora var. Torreyana
***Acacia Willardiana
**Coursetia glandulosa
**Acacia Farnesiana
**Caesalpinia pumila
**Phaulothamnus spinescens
*Acacia occidentalis
*Jacquinia pungens
*Guaiacum Coulteri
*Randia Thurberi
*Fouquieria peninsularis
*Lemaireocereus Thurberi
*Vallesia glabra
*Desmanthus Covillei
*Ruellia californica
Lippia Palmeri
Echinopterys eglandulosa
Lycium carinatum
Cordia sonorae
Opuntia fulgida
Forchammeria Watsoni
Pachycereus pecten-aboriginum

Among the hills near Guaymas the borders of streamways support heavy stands of shrubs and small trees, particularly in valleys which face the Gulf. In these communities a few species are more abundant than others but there are no true dominants. The composition varies from place to place, and some of the plants are represented by very few widely separated individuals. Among these are several plants not found elsewhere in the latitude of Guaymas or north of there. At Bahía San Carlos and Miramar the following plants have been found in the slightly moist situations:

**Prosopis juliflora var. Torreyana
**Lysiloma divaricata
**Pithecellobium sonorae
**Sapindus Saponaria
*Maytenus phyllanthoides
*Lantana Camara
*Gossypium Davidsonii
*Eupatorium sagittatum
*Mascagnia macroptera
*Franseria ambrosioides
Cordia sonorae
Sapium biloculare
Anisacanthus Thurberi
Vitex mollis
Ruellia californica
Stegnosperma halimifolium
Bumelia occidentalis
Forchammeria Watsoni
Beloperone californica
Vallesia glabra
Viscainoa geniculata
Pisonia capitata
Colubrina glabra
Washingtonia robusta
Zizyphus sonorensis
Acacia Farnesiana
Euphorbia colletioides
Bursera confusa
Abutilon californicum
Benthamantha Wrightii
Cordia brevispicata
Hintonia latiflora

On the thin soil of inland slopes the vegetation is open and very xeric. The slopes rising from small bays and inlets are like those of the interior. The low cover is relatively dense only on slopes that are dominated by xeric semishrubs or *Hechtia*, above which rise widely spaced trees, cacti, or *Fouquieria*. In several

localities northwest of Guaymas and within 5 km. of the coast the following species have been found to predominate:

***Bursera microphylla
***Fouquieria peninsularis
***Acacia Willardiana
***Jatropha cinerea
***Jatropha cuneata
***Hechtia montana
**Haplopappus sp.
**Citharexylum flabellifolium
**Bebbia juncea
*Agave Schottii
*Lemaireocereus Thurberi
*Lycium brevipes
*Krameria parvifolia
Ferocactus alamosanus
Carlowrightia californica
Porophyllum pausodynum
Echinocereus scopulorum

Quiet shores of inlets and lagoons are bordered by *Rhizophora Mangle* and *Avicennia nitida*, but there are no extensive areas of these trees. East of Guaymas are several hundred hectares of saline flats very sparsely covered with *Suaeda ramosissima*, *Allenrolfea occidentalis*, *Wislizenia Palmeri*, and *Aster parviflorus*. On the outwash slopes immediately inland from the saline flats is the heaviest stand of *Pachycereus Pringlei* known on the Sonoran coast. It rivals in density the stands at the head of Bahía Concepción, in Baja California, but the individuals are neither so large nor so much branched. *Pachycereus* is here made very conspicuous by a white coating of dung of sea birds which roost on the tops.

Guaymas is cited as the type locality for a large number of plants, a fact which has given rise to the impression that there is a high degree of endemism in the flora of its environs. The circumstance is due largely to the fact that the Guaymas region was far more accessible than any other locality in central Sonora until about 1900, and was the first place visited by active collectors. Very many of the plants first found at Guaymas are now known to have a wide distribution in central and southern Sonora or even in Sinaloa. There remain, however, perhaps 40 species which are not known outside a radius of 50 km. around Guaymas.

Gulf coast of Baja California. North of the Cape Region the Gulf coast of Baja California is the most thinly settled part of the Sonoran Desert, because of the lack of arable soil and the absence of favorable places for the development of water supplies. Almost the entire coast is poorly known and difficult of access by land. A road leads from Mexicali, on the international boundary, to Bahía San Felipe, a distance of 200 km. The coast may be reached from the interior by saddle from Marmol to Miramar (Punta Santa Isabel), by road from Punta Prieta to Bahía Los Angeles, and by road from Pozo Alemán to Barril. The only road paralleling the coast runs from Santa Rosalía to the mouth of Bahía Concepción. All these routes have been traversed in the present work, and the coast has been closely followed by boat from Isla Carmen to La Paz.

The only rainfall data for the coast are those for Santa Rosalía, Mulegé, and La Paz. The northern part of the coast, in the rain shadow of the Sierra Juárez and Sierra San Pedro Mártir, is undoubtedly the driest, and its precipitation is

probably below an annual mean of 75 mm. (3 in.). At Santa Rosalía the mean annual rainfall is 138 mm. (5.43 in.), and at Mulegé 104 mm. (4.09 in.).

In spite of the uniformly low rainfall along the entire coast, there is a notable change in the vegetation between Bahía Los Angeles and Barril. This is associated with the change from winter to summer incidence of the principal percentage of the light and uncertain precipitation, and also with the limitation of frost to brief and infrequent periods. The dominant perennials and many of the herbaceous ephemerals of the Lower Colorado Valley persist as far south as Bahía Los Angeles. The large perennials of the sarcophyllous desert (Vizcaíno Region), which is adjacent on the west, either are absent from the Gulf coast north of Bahía Los Angeles or are confined to small favorable habitats. *Pachycereus Pringlei* and *Bursera microphylla* range sparingly as far north as Bahía San Felipe. Near Bahía Los Angeles, *Idria* approaches the coast only in gravelly bottoms of streamways, and *Pachycormus* only on south slopes of boulder-covered hills. *Fouquieria splendens* ranges south to Bahía San Bartolomé; *Larrea* persists on deep, level soils as far south as Bahía Concepción; and *Cercidium microphyllum* extends to Bahía Concepción. With these exceptions the vegetation of the Central Gulf Coast is made up of species which do not occur in abundance north of Bahía Los Angeles. The change in the aspect of the vegetation is from widely spaced slender shrubs to widely spaced shrubs and small sarcocaulescent trees. The dominants are *Jatropha cuneata*, *Fouquieria peninsularis*, *Bursera microphylla*, *Jatropha cinerea*, and *Bursera Hindsiana*.

Immediately north and south of Bahía Los Angeles the coast is bordered by short ranges of hills very lightly clothed with vegetation. To the west of them, and on or near the median line of the peninsula, are Sierra Calamajué (1658 m.), Sierra Yubay (800 m.), and Sierra San Borjas (1200 m.). Between the coastal hills and these mountains are two valleys, 30 and 75 km. long, comprising the Desierto de San Julián, the Desierto de Santa María, and the Llano de San Pedro. These are enclosed basins, the bottoms of which are subject to overflow at very rare intervals. The bottoms are devoid of plants, and the surrounding floors bear only widely scattered individuals of *Atriplex Barclayana*. The slopes of the hills bordering these basins are almost devoid of woody perennials. The landscape here comes nearer than any other in the Sonoran Desert to fitting the European definition of desert as a place with no plants whatever.

On the Gulf coast east of Calmallí, between Cabo San Miguel and Punta San Juan Bautista, long outwash slopes fall from the interior to the coast. The dominant plants on these slopes are *Larrea*, *Bursera microphylla*, and *Fouquieria splendens*. *Fouquieria* is less abundant than *Larrea* or *Bursera*, but is conspicuous by reason of its size and branching. The mature individuals are 7 to 9 m. high, with very stout branches which fork frequently at the top. The slender tips of the main arms and branches are gracefully dependent and sinuously curved. This locality is near the southern limit of *Fouquieria splendens* in Baja California, and the specimens here contrast strongly with the small plants along its eastern distributional limit, with their straight, slender, unbranched arms.

The simple vegetation of the bajadas in this locality forms a 15 per cent cover, and its composition is as follows:

***Larrea tridentata
***Bursera microphylla
***Fouquieria splendens
***Jatropha cuneata
***Opuntia cholla
**Olneya tesota
**Bursera Hindsiana
**Opuntia clavellina
Viscainoa geniculata
Fouquieria peninsularis
Ferocactus horridus
Pedilanthus macrocarpus
Pachycereus Pringlei

The influences of slope exposure are responsible for very general differences in vegetation between north and south slopes in the Central Gulf Coast subdivision. Where the same type of rock and soil is involved, the north slopes have a slightly heavier stand of perennials. *Idria* and *Pachycormus* are occasionally found on north slopes although absent from south slopes and level ground. The southern limit of *Idria* is on the north slopes of Cerro Tres Vírgenes, and it is not found on the south slopes. No cases have been observed in which west slopes, facing the Pacific, bear heavier vegetation than adjacent east slopes. Ready access of storms and moist winds from the ocean are of great importance in differentiating the Central Gulf Coast from the Vizcaíno Region, but they do not outweigh the importance of orientation toward or from the midday sun. The abundance of the epiphytic *Tillandsia recurvata* on the desert trees and shrubs in the Vizcaíno Region is an indication of recurrent periods of moist air, but the plant is rare in the interior hills and absent from the Gulf slopes. The influence of the Pacific Ocean on the vegetation of the Gulf coast could scarcely be less if the ocean were 1000 km. away instead of 70 to 100 km.

South of Cerro Tres Vírgenes as far as Bahía Concepción, the drainage divide of the peninsula lies between 500 and 1000 m., with a number of peaks and mesas of higher elevation. Precipices, steep slopes, and strongly tilted bajadas characterize the slopes draining into the Gulf. The landscape is dominated by evidences of recent volcanism. It is stated by the inhabitants that the Tres Vírgenes volcano was in eruption in 1790 (pl. 27). Malpais fields cover large areas, and partially aggraded slopes have a rocky surface and thin soil heavily banded with caliche. The hanging talus which is occasionally seen in Arizona and Sonora (pl. 3, fig. 2) is very common here. In some of the higher valleys the volcanic surface is covered with sand, which is evenly distributed and never accumulated in dunes.

In the area under consideration there is a slightly heavier cover of vegetation at 500 m. elevation than there is on the slopes near the shore of the Gulf. The coverage in the two situations is approximately 20 per cent and 10 per cent respectively. The composition at the higher elevation is richer, but many of the perennials found there are sporadic in occurrence. This is true of common species —*Olneya tesota*, *Encelia farinosa*, *Koeberlinia spinosa*, *Viscainoa geniculata*, *Simmondsia chinensis*, and others—as well as of woody and herbaceous perennials, which are nowhere abundant.

There is a notable scarcity of pure stands or even of communities strongly dominated by two or three species. At all elevations and in nearly all habitats the vegetation is mixed, even if it is very open. The exceptions are small valleys with a level surface and a deep soil overlaid by sand or sandy clay. In these, *Larrea* forms from 80 to 95 per cent of the stand. A single valley about 2 km. wide was seen in which exceptionally large plants of *Encelia farinosa* formed a nearly pure stand.

The following list indicates the composition and relative abundance of the vegetation on the upper slopes of the Gulf coast in the area between Cerro Tres Vírgenes and Arroyo Santa Agueda, which debouches just south of Santa Rosalía.

***Larrea tridentata
***Jatropha cuneata
***Opuntia clavellina
***Franseria magdalenae
***Bursera microphylla
***Fouquieria peninsularis
***Opuntia cholla
**Jatropha cinerea
**Cercidium floridum
**Opuntia calmalliana
**Agave sobria
*Pachycereus Pringlei
*Lycium brevipes
*Machaerocereus gummosus
*Viscainoa geniculata
*Prosopis juliflora var. Torreyana
*Franseria Bryantii
*Opuntia invicta
*Simmondsia chinensis
*Krameria parvifolia
*Haplopappus sonoriensis
Pedilanthus macrocarpus
Solanum Hindsianum
Petalonyx linearis
Atamisquea emarginata
Cercidium sonorae
Bebbia juncea
Acalypha californica
Stillingia linearifolia
Melochia tomentosa
Berginia virgata
Ruellia californica
Cassia confinis

The borders of the shallow streamways of the Tres Vírgenes region support only a slightly heavier stand of large perennials than the general surface does. The habitat is characterized by *Prosopis juliflora* var. *Torreyana*, *P. Palmeri*, *Olneya tesota*, and *Cercidium floridum*, but the principal cover is formed by the shrubs *Hymenoclea pentalepis*, *Bebbia juncea*, *Haplopappus sonoriensis*, *Beloperone californica*, and *Horsfordia Newberryi*.

The middle courses of the streamways which descend across the Gulf slopes are often deeply cut, occupying small barrancas from 10 to 200 m. in width. The floors and banks of these small valleys afford moisture conditions favorable enough to support an open stand of small trees, often accompanied by nearly closed shrubbery. Here the sarcocaulescent trees yield the dominance to microphyllous leguminous trees. The commonest of the latter is *Lysiloma candida*, a slender tree of *Acacia* form with very light-colored bark. Because of the value of its inner bark for tanning, this is the most useful native plant of the peninsula. Cutting has reduced the number of large trees in many localities, but second growth from stumps maintains its original local distribution.

The plants characteristic of the small barrancas are:

***Lysiloma candida
**Prosopis juliflora var. Torreyana
**Vallesia glabra
**Euphorbia californica
**Lantana Camara
*Prosopis Palmeri
*Mascagnia macroptera
Condalia globosa
Hyptis laniflora
Berginia virgata
Ficus Palmeri
Brongniartia peninsularis
Stegnosperma halimifolium
Aeschynomene nivea
Thryallis angustifolia

A very different picture is presented by the lower courses of the large streams which have descended nearly to sea level. High water is rare and brief in these streams, but the floods are extremely violent on account of the steep gradient of the upper tributaries. Among these streamways are the Arroyo Reforma, Arroyo Santa Agueda, Arroyo San José, and Río Magdalena. The Arroyo Reforma has a broad, sandy bed, and the Río Magdalena, which drains the north slopes of Sierra de Zacatecas, crosses the coastal plain as a series of sandy beds meandering among islands of sand and boulders, the whole having a width of nearly 3 km.

The vegetation of the broad stream beds is confined to (1) upland trees and shrubs which are well enough rooted to withstand the floods, (2) short-lived shrubs of species characteristic of such habitats, and (3) small perennials of rapid growth. All these are distributed in extremely irregular fashion. Common in the three groups respectively are:

(1) Lysiloma candida
Prosopis juliflora var. Torreyana
Cercidium floridum
Pithecellobium confine
Sapium biloculare

(2) Hymenoclea pentalepis
Haplopappus sonoriensis
Hyptis laniflora
Bebbia juncea
Aster spinosus

(3) Fagonia californica
Nicotiana trigonophylla
Sympetaleia aurea
Cassia confinis
Sphaeralcea Hainesii
Hofmeisteria fasciculata var. pubescens
Physalis crassifolia

The section of the Gulf coast lying between Mulegé and Canipolé embraces the area around Bahía Concepción and is the broadest part of the coastal belt. North and west of Mulegé are large, nearly level bajadas with sandy surface. On both sides of Bahía Concepción hills closely approach tidewater, occasionally separated by wedges of bajada or canyon floor. In spite of the low rainfall indicated by the record for Mulegé (4.09 in., 104 mm.), the vegetation of the bajadas in its vicinity is slightly taller and denser than it is north of Santa Rosalía, and the vegetation of the hills is approximately twice as dense, as well as richer in small trees. It is difficult to account for this contrast except on the possibility that the Mulegé record is not truly representative of the adjacent region, or else that the

mean precipitation on the coast north of Santa Rosalía is lower than the 138 mm. recorded for that town, which may well be the case.

On the sandy bajadas north of Mulegé the vegetation forms a coverage of 30 to 40 per cent and is much more uneven in its height as well as its color tones than the bajada communities which are strongly dominated by *Larrea*. Trees are commonest at the upper edges of the bajadas and along the streamways. *Pachycereus Pringlei* is frequent on the lower bajadas, increases in abundance rapidly as they are ascended, and remains abundant on the lower slopes of the parent hills. Its role in the vegetation is very much the same as that of *Carnegiea* in the Arizona Upland and that of *Idria* in the Vizcaíno Region. Several cylindropuntias are common on the lower bajadas, particularly *Opuntia cholla*, which closely resembles in every respect the equally abundant *Opuntia fulgida* of the northern subdivisions of the Sonoran Desert.

On representative areas of sandy or gravelly bajada away from streamways, the composition of the vegetation in the Mulegé region is as follows:

***Jatropha cuneata
***Larrea tridentata
***Bursera microphylla
***Encelia farinosa
***Opuntia cholla
**Fouquieria peninsularis
**Colubrina glabra
**Jatropha cinerea
**Pachycereus Pringlei
**Cercidium microphyllum
*Opuntia ciribe
*Lycium brevipes
*Pedilanthus macrocarpus
*Simmondsia chinensis
Solanum Hindsianum
Machaerocereus gummosus
Condalia globosa
Opuntia invicta
Bursera Hindsiana
Olneya tesota
Trixis californica

The universally rocky slopes in the vicinity of the mouth of Bahía Concepción differ from the bajadas far more in their physiognomy than in their composition. The plant covering of the hills is open or extremely sparse, varying in density with the gradient of the slopes and the amount of soil which they afford. *Fouquieria peninsularis* is the most conspicuous of the abundant plants, and *Jatropha cuneata* is the commonest. *Bursera microphylla* and *Cercidium microphyllum* are common, but seldom greatly exceed the shrubs in height. *Pachycereus* is infrequent, and other cacti are far less common than on the bajadas. *Larrea* is very infrequent on the slopes and often absent over large areas. Plants which are common on the slopes and infrequent on the bajadas include the following, for which the relative abundance would be difficult to determine:

Abutilon Palmeri
Acalypha saxicola
Atamisquea emarginata
Bebbia juncea
Bourreria sonorae
Cercidium sonorae
Ditaxis Brandegei
Echinocereus Brandegei
Euphorbia tomentulosa
Fagonia californica
Ferocactus rectispinus
Lemaireocereus Thurberi

Opuntia ciribe
Peucephyllum Schottii
Pithecellobium confine
Porophyllum gracile
Randia Thurberi
Ruellia californica
Viguiera deltoidea

Bahía Concepción is 40 km. long and varies from 5 to 10 km. in width. Bluffs, inlets, and islands make the shore-line topography of the north half of the bay intricate and picturesque. In the south half the shores are low and continuous. There are numerous colonies of *Rhizophora Mangle* in quiet corners of the bay. In the northern section the typical vegetation of the slopes and valley bottoms descends nearly to the water. The only woody plant definitely confined to the vicinity of the shore is *Maytenus phyllanthoides*, which in some spots forms 20 per cent of the stand. On the west side the slopes which drain into the bay rise for 15 to 20 km. to the summit of Sierra de Zacatecas, where there is a considerable area over 1000 m. Four large canyons, as well as several small ones, enter the bay from the west. The largest of these is Arroyo Codeje. On the east and at the head of the bay there are no important affluents. There is an area of alluvial bottom land at the mouth of Arroyo Codeje covered by a heavy forest of *Prosopis juliflora* var. *Torreyana* and *Lysiloma candida*. Farther south, the alluvial flats near the bay are covered with thickets of *Maytenus phyllanthoides* or are nearly bare, supporting only scattered plants of *Allenrolfea occidentalis* and *Frankenia Palmeri*. On the inner edge of the alluvial land at the south end of the bay is the heaviest stand of *Pachycereus Pringlei* seen in Baja California. In the center of the area there are magnificent examples of this massive cactus from 12 to 14 m. in height, well branched and growing in an unusually close stand.

South of Punta Pulpito, due east of the head of Bahía Concepción, the coast is closely followed by the escarpment which forms the eastern slope of Sierra de la Giganta. The true desert is here confined to a narrow and interrupted band along the coast, to the low salient ridges of the mountains, and to the islands which hug the coast. The vegetation of the canyon slopes and the steep, rocky beds of the streamways of Sierra de la Giganta belongs to the type of thorn forest characteristic of the Cape Region.

East of La Paz and southward along the Gulf, the vegetation is desert on volcanic soils and thorn forest on the granitic bajadas which descend sharply from the Sierra de la Laguna and Sierra de San Lazaro. In aspect and composition this southernmost tip of the Sonoran Desert closely resembles the region around Bahía Concepción.

On the stony volcanic bajadas and slopes east and southeast of La Paz, most of the vegetation is very open, forming a cover of only 10 to 15 per cent. Few of the trees exceed 4 m. in height, and *Pachycereus* is small and unbranched. The composition here is:

***Jatropha cuneata
***Fouquieria peninsularis
***Opuntia cholla
**Bursera microphylla
**Acacia californica
**Machaerocereus gummosus

*Cyrtocarpa edulis	Caesalpinia arenosa
*Ruellia peninsularis	Encelia farinosa
*Euphorbia californica	Solanum Hindsianum

Vizcaíno Region

(Sarcophyllous Desert. Agave-Franseria Region)

The lofty, uniform crest of Sierra San Pedro Mártir terminates abruptly just north of the 30th parallel. North of this latitude Baja California has three longitudinal belts of very dissimilar vegetation: chaparral on the coast and westerly slopes, coniferous forest on the mountains, and desert on the Gulf coast. South of this latitude, as far as the northern end of Sierra de la Giganta, the peninsula is desert from coast to coast. South of Sierra San Pedro Mártir the peninsula maintains a fairly uniform width of about 80 km. for a distance of 250 km. It then widens, with a long triangular projection on the Pacific coast, and has its maximum width of 200 km.

The Vizcaíno Region comprises the Pacific drainage of central Baja California from the southern end of Sierra San Pedro Mártir south nearly to latitude 26° N. The designation of this subdivision of the Sonoran Desert is an extension of the use of the name "Vizcaíno Desert," which has long been applied to the plains which occupy the long triangular projection. The Vizcaíno Region includes the rough mountainous interior as well as the Vizcaíno Desert and the additional wedge of coastal plain which extends south to Punta Pequeña.

The great escarpment which is so well defined in northern and in southern Baja California is less clearly marked in the central section, but has served nevertheless to place the drainage divide much nearer the Gulf than the Pacific. The backbone of the peninsula is here formed by Sierra Calamajué, Sierra San Borjas, and Sierra Calmallí. Only a few peaks in these ranges are over 1500 m. in elevation. From Rosario to Calmallí the face of the country is very rugged. The larger mountains run nearly parallel to the axis of the peninsula, the volcanic hills and mesas are very irregular in position, and the level areas with deep soil are few and small even along the coast. A single enclosed basin drains into Laguna Seca Chapala at latitude 29° 25′ N. Approximately 40 per cent of the area north of the Vizcaíno plain lies below 500 m.

On the southern edge of the Vizcaíno cape are two small ranges of grotesquely built mountains, Sierra Pintada and Sierra Santa Clara. If they are left out of account, the rugged axis of Baja California may be pictured as extending with uniform width throughout the Vizcaíno subdivision. Its increased width between latitudes 27° and 28° is chiefly due to the featureless plains of the Vizcaíno Desert and those in the vicinity of Laguna de San Ignacio.

Very little is definitely known about the climatic conditions of the Vizcaíno Region, as there are no official records from it. The summer temperatures of the immediate coast are greatly reduced as compared with those of the interior. The rainfall is almost wholly in the winter and early spring. At long intervals there

are summer storms south of the Vizcaíno plain. According to the inhabitants, the winter rainfall is extremely variable from year to year. When the peninsula was visited in 1934 it was very dry, and the residents in several localities stated that it had been seven years since there had been good rains. On the visit of 1935, heavy rains were encountered in February, and the condition of the plants indicated that rain had begun several weeks before. Some of the same informants then alleged that the rains had not been so copious for twelve years. Whatever the conditions may be from January to April, the remaining eight months of the year are almost invariably dry throughout the Vizcaíno Region. During spring and summer there is morning fog along the coast as far south as the Vizcaíno plain, and it extends inland wherever there is a low coastal shelf for a distance of 5 to 6 km. Foggy mornings are said to be most frequent in July and August. A strong wind from the Pacific whips the coast during the day and early part of the night, and is apparently continuous throughout the year.

The vegetation of the Vizcaíno Region comprises relatively heavy stands of large perennials, including some of its most striking plants, in communities of rich composition. It also comprises every phase of the impoverishment of these outstanding communities, some of the impoverished ones being areally the most important. Finally, there are great areas of salitral in the Vizcaíno plain on which there is an extremely scanty cover of halophytic plants.

On purely observational evidence it is possible to determine some of the features which control the conditions underlying the vegetational differences. Six features seem to be particularly important:

Physiography: The greatest contrast in the area is between the mountainous axis of the peninsula and the alluvial deposits of the Vizcaíno plain.

Proximity to the sea: This means little with respect to rainfall, humidity, or soil moisture. The extreme coastal belt is invariably open and barren on account of the incessant high wind.

Character of substratum: This is important in differentiating the vegetation of small areas of deep soil from that of large areas of shallow soil, as well as in making a difference between the vegetation of volcanic soils, that of granitic soils, and that of sand.

Altitude: There is little in which this composite condition outweighs the others. Probably some of the high mesas are visited by winter temperatures which are hostile to some of the common plants. There is nothing to indicate that the precipitation increases appreciably with altitude on the small and low mountains of this region. The principal characteristics of the vegetation at higher levels are low stature, simple composition, and absence of several of the large lowland dominants. These features may be due to high wind and shallow soil as much as to any of the conditions commonly attributable to small increases in elevation.

Water supply: In general the streamways of the Vizcaíno Region make little impress upon the vegetation, but springs or places with a constantly generous supply of water are as striking as they are rare. In every case observed, the limited

area of moist soil was heavily clothed with plants, including rare perennials of the region and also extralimital plants at the north or south edge of their ranges.

Orientation of slope: Under comparable conditions of substratum there is an almost universal difference in vegetation between slopes facing north and south. In some places the difference is more conspicuous than in others, depending on the dominants involved, but it can always be detected by careful examination. At the higher elevations the difference in composition on opposed slopes is greater, although sometimes not involving any of the large perennials. On hills lying within 4 or 5 km. of the coast there is a marked difference in vegetation between the slopes facing the sea and those facing inland. The windward slopes are usually without any large perennials and may be scantily covered with low perennials or may be so bare of them that the yellow lichens covering the rocks give the entire slope their color, conspicuous for several kilometers. The lee slopes of coastal hills are closely similar to the inland ones.

Northern Vizcaíno Region. In the northwestern corner of the Vizcaíno Region the vegetation is influenced in physiognomy and composition by the chaparral of the northwestern coast, which is here giving way to desert. The writer has described elsewhere the transition between these formations (Shreve, 1936) and the extension of certain chaparral plants southward into the desert. Some of the plants which are dominant a little farther south are just making their appearance, and some of the widespread desert plants are absent, although well represented in the northeastern corner of the area.

The predominant surfaces in the northern Vizcaíno Region are low, maturely worn hills and gently rolling slopes with 10 to 20 cm. of stony soil and a surface accumulation of coarse fragments. On certain types of basaltic rock the soil is a very fine rusty-red clay of greater depth. The nearly level areas usually have a stony loam soil or less commonly a fine sandy loam. The steep hillsides are either bare or covered with large stones supporting pockets of soil.

On the gentle slopes with loam soil the most abundant plant is *Franseria chenopodifolia*. In many places it outnumbers all other plants combined, and its silvery gray foliage blankets the landscape. The plants have a very uniform height of 5 to 7 dm. and a low spread of branches which covers a little less than a square meter in mature plants. *Franseria chenopodifolia* is very abundant in the desert-chaparral transition, but in the Vizcaíno Region it wanes rapidly on approaching the drainage divide of the peninsula. It is a facultative evergreen and distinctly of the desert rather than the chaparral type. A few desert perennials are lower than *Franseria*, but the majority of its associates protrude well above the canopy which it forms. The well closed appearance which it sometimes gives the vegetation would be greatly altered if all the Franserias were removed, for the associates alone would seldom make more than a 15 per cent cover.

Several of the conspicuous and abundant plants of the Vizcaíno Region reach their northern limits in the southern part of the desert-chaparral transition, including *Machaerocereus gummosus*, *Myrtillocactus cochal*, *Idria columnaris*, *Yucca*

valida, and *Pachycereus Pringlei*. Throughout the northernmost part of the Vizcaíno Region all these except *Idria* are infrequent or found only in small colonies. *Idria* at once becomes abundant on gentle south slopes, but does not here reach its maximum size.

On the heavy red clay *Franseria chenopodifolia* is very uncommon and *Franseria camphorata* is extremely abundant. The latter is a small plant of 2 to 3 dm. with gray, fernlike leaves. Its presence is a sure indication of extremely fine volcanic clay. It is known outside Baja California only at a single station on this type of soil near the south end of Sierra Picú, in the District of Altar, Sonora.

The characteristic plants of the prevalent volcanic soils in the northern part of the Vizcaíno Region are:

****Franseria chenopodifolia
****Franseria camphorata
***Agave Shawii
**Viguiera deltoidea
**Encelia farinosa
**Fouquieria splendens
**Simmondsia chinensis
**Eriogonum fasciculatum
**Opuntia prolifera
**Ephedra californica
*Idria columnaris
*Yucca valida
*Pachycereus Pringlei
*Machaerocereus gummosus
*Myrtillocactus cochal
*Larrea tridentata
*Encelia californica
*Atriplex polycarpa
Ferocactus acanthodes
Opuntia ciribe
Euphorbia misera
Agave deserti
Yucca Whipplei
Euphorbia tomentulosa
Salvia Munzii

The broad-leaved sclerophylls which characterize the chaparral have all but disappeared in the northern Vizcaíno Region, being represented only by *Rhus laurina*, *R. integrifolia*, *Rhamnus crocea*, and *Prunus fasciculata*, all of which are confined to moist situations. On steep north slopes are found a few of the large perennials which are abundant in the desert-chaparral transition, but are not of the chaparral type. These include the deciduous *Aesculus Parryi*, *Galvezia juncea*, *Cneoridium dumosum*, and *Isomeris arborea*, and the green-stemmed leafless *Adolphia californica*.

About halfway across the peninsula from the Pacific coast, and also at elevations above 500 m., the aspect of the vegetation begins to change, chiefly because of the reduction in numbers of *Franseria chenopodifolia* and *Agave Shawii*. New shrubs and cacti begin to prevail, along with some of the more xeric dominants, including *Larrea*, *Cercidium microphyllum*, and *Olneya*. *Yucca valida* and *Pachycereus Pringlei* remain infrequent, but *Idria* is abundant on north slopes. No one plant strongly dominates the vegetation. The density of the shrubs 1 m. or more in height ranges from 40 per cent on deep soil to 15 per cent or less on gentle slopes with shallow soil. Except *Pachycereus* and *Idria*, there are no perennials over 4 or 5 m. in height.

A record follows of the vegetation in localities near latitude 30° N. on the

thin loam soil of gentle volcanic slopes and plains above 500 m. elevation and near the median line of the peninsula.

**Larrea tridentata
**Agave deserti
**Franseria dumosa
**Encelia farinosa
**Opuntia prolifera
**Atriplex polycarpa
**Viguiera deltoidea
**Fouquieria splendens
**Eriogonum fasciculatum
*Simmondsia chinensis
*Ephedra aspera
*Opuntia ciribe
*Cercidium microphyllum
*Coldenia canescens
*Condalia lycioides
Franseria chenopodifolia
Krameria Grayi
Yucca valida
Lycium brevipes
Condalia spathulata
Ferocactus acanthodes
Yucca schidigera
Eurotia lanata
Calliandra californica
Acacia Greggii
Echinocereus Engelmannii
Fagonia californica

Hills of granite or gneiss occur at a number of localities in the northern Vizcaíno Region, but the total area covered by them and their derived soils is small. The granite plains, with their rounded boulders and light-colored surface of coarse angular sand, afford a background very unlike the prevailing one. Also the vegetation has several distinctive features. The composition is rich and the species are thoroughly intermingled. A high percentage of the plants are large, and many of them have reached the maximum size of their kind. The cover is variable in density and height. Close stands of shrubs, small colonies of *Agave*, or groups of cacti alternate with meandering bare areas of clean, hard sand. *Larrea* here reverses its behavior in other parts of the Sonoran Desert and is more abundant on granite soils than on volcanic. *Pachycormus discolor* and *Viscainoa geniculata* reach their northern limit for the west side of the peninsula on the granite plains. In spite of the evidence that moisture conditions are slightly better on the granite soils, the latter are not colonized by any of the southward-ranging plants of the desert-chaparral transition except *Franseria chenopodifolia*, which is indeed as much a plant of the desert as of the transition.

The composition of the communities on granitic sandy loam is as follows:

***Encelia frutescens
***Franseria chenopodifolia
***Viguiera deltoidea var. tastensis
**Larrea tridentata
**Opuntia ciribe
**Atriplex polycarpa
**Idria columnaris
**Eriogonum fasciculatum
**Agave deserti
**Lophocereus Schottii
*Prosopis juliflora var. Torreyana
*Lycium californicum
*Simmondsia chinensis
*Eurotia lanata
Franseria dumosa
Encelia californica var. asperifolia
Trixis californica
Viscainoa geniculata
Ephedra californica
Bursera Hindsiana
Solanum Hindsianum
Franseria magdalenae

Beloperone californica	Crossosoma Bigelovii var. glaucum
Ferocactus viscainensis	Isomeris arborea
Acalypha californica	Abutilon Palmeri
Pachycormus discolor	

The Vizcaíno Region is the only part of the Sonoran Desert in which sarcophyllous plants are abundant. They are represented by several species of *Agave*, *Dudleya*, and *Mesembryanthemum*, the commonest of these being *Agave Shawii* and *A. deserti*. The former is a large plant with leaves 5 to 8 dm. long and inflorescences 2 to 3 m. high. In many localities near the coast this is one of the dominant plants, particularly on deep, somewhat sandy soils. Toward the center of the peninsula the heavy stands become more local, and near the divide it is seldom seen. The high percentage of plants with flower stalks indicates that *Agave Shawii* is short-lived, probably blooming at the age of 15 or 20 years. In every colony there are many dead plants with leaves and flower stalks in the living position, many leaning and fallen ones, and still other rosettes of old leaves in various stages of decay. Throughout the North American Desert the vegetation as a whole has a neat and well kept appearance, due to the rapid decay of the few defunct plants and fallen parts. The heavy stands of *Agave Shawii*, littered with fallen and decaying plants, are the most untidy of all the desert communities. No evidence was found that the fallen carcasses of *Agave* afford favorable spots for germination and early growth of their associates.

Agave deserti is a smaller plant than *A. Shawii* and grows either singly or in groups and rows. It never forms pure stands, but is a common plant on all but the finest soils throughout the Vizcaíno Region. *Mesembryanthemum* is limited to the extreme coast, and the several species of *Dudleya* shade from abundance near the coast to infrequency in the interior.

Twenty-three species of *Agave* have been credited to Baja California, many of them poorly known. The ecological prominence of the genus in Baja California is matched only by the extensive stands of *A. lechuguilla* in Coahuila. All the sarcophylls are absent or very local in other parts of the Sonoran Desert. It is difficult to obtain any evidence indicating why the Pacific coast is a favorable locality for this life form. The one feature in which the coastal strip differs from the rest of the Sonoran Desert is the frequent visitation by fog and the many periods of high relative humidity. The zone affected by these conditions is accurately marked in the Vizcaíno Region by the abundance of *Tillandsia recurvata*, which is not so widely distributed, however, as *Agave deserti*. Not enough is known about the requirements and ecological life history of *Agave* to help in the solution of this problem.

South of Cataviñá, high mesas and rolling plateaus stretch eastward toward Cerro Ugarte (1386 m.) and extend with little change as far south as Laguna Seca Chapala. At 500 to 1000 m. this area is characterized by a low, open cover or by very simple stands of shrubs. In the deeper soil of valley bottoms *Larrea* and *Atriplex polycarpa* form a 20 per cent cover with very few associates. On the bajadas and gentle stony slopes these plants are joined by *Franseria chenopodifolia*

and *Lycium californicum*, in a slightly heavier stand which includes occasional individuals of the plants listed below. On the thin soil of somewhat steeper slopes the vegetation is low but denser. There are many areas of 100 sq. m. on which there are no plants more than 5 dm. high. The few individuals of *Idria* and *Pachycereus* are small. The trees common at lower elevations are infrequent here, and *Ferocactus* and *Echinocereus* are more abundant than *Opuntia*.

The plants characteristic here are:

Larrea tridentata
Atriplex polycarpa
Franseria chenopodifolia
Lycium californicum
Agave deserti
Viguiera deltoidea
Haplopappus sonoriensis
Fouquieria splendens
Ferocactus acanthodes
Lycium brevipes
Eriogonum fasciculatum
Yucca Whipplei
Ferocactus viscainensis
Echinocereus maritimus
Simmondsia chinensis
Ephedra aspera
Krameria parvifolia

Southern Vizcaíno Region. On traveling south in Baja California, gradual but continuous changes in the plant life are observable. Among the most impressive are the first appearances of *Idria*, *Pachycereus*, *Yucca valida*, and other plants which mark the entrance into the Vizcaíno Region at the north. Equally noticeable are the changes in the character of the plant communities. Plants which at first are rare become common, plants which are confined to definite habitats in the north become ubiquitous, large and well developed individuals of dominant species become more frequent, and the number of localities increases in which there is a diversified stand with members of many life forms.

There is no particular latitude at which the vegetational change is most obvious. The elevation and the character of the soil constantly influence the change, and in many localities there is a sharp return to poor and simple communities, apparently owing to topographic reduction of rainfall.

The broad boundary between the northern and southern parts of the Vizcaíno Region lies on the descent from Laguna Seca Chapala to Punta Prieta. In this distance of 50 km. there are no important floristic changes, but there is a very noticeable enrichment of the vegetation. In the long granitic valley which descends to Punta Prieta from the north, and on many of the higher volcanic plains and mesas of the neighboring region, are to be found some of the outstanding communities of Baja California. Among them are rich assemblages of many of the striking plants which have given the peninsula its reputation as a botanical wonderland.

Here, as in all other parts of the desert, the landscape is dominated by a few large species, which are usually greatly outnumbered by some of their smaller associates. A strong individuality is given the vegetation of the southern Vizcaíno Region by *Idria columnaris*, *Pachycormus discolor*, *Agave Shawii*, *Pachycereus Pringlei*, and *Yucca valida*. Rarely is their combined total more than 20 per cent of the population. Although these five perennials are closely associated, it is

uncommon for them to occur in nearly equal abundance in any one restricted area. *Idria* and *Pachycereus* are the most general in occurrence, a fact which indicates that they are the most catholic members of the group in their habitat requirements. Indeed, it is remarkable that five plants exemplifying such dissimilar life forms are so often able to reach their greatest size and finest development under the same conditions of climate and soil.

Idria and *Pachycereus* often attain a height of 14 m., and several exceptional examples have been measured which were over 20 m. *Pachycormus* is commonly 5 to 8 m. high and rarely exceeds the latter height. On the immediate coast and in some of its least favorable inland habitats, *Pachycormus* is a prostrate and grotesquely formed tree with a very thick trunk tapering abruptly into normal slender terminal branches. Trees of this type have commonly been selected by travelers to illustrate *Pachycormus* (Goldman, 1916). Over most of its inland range, however, it is an erect and shapely tree. The basal diameter of the trunk is always greatly exaggerated for a tree of such low stature, and it tapers rapidly among the branches. The smooth, light bark contrasts strongly with the dark foliage to make it a highly ornamental tree. In very rainy seasons *Pachycormus* is heavily infested with *Cuscuta Veatchii*, which, with no vestige of a connection with the ground, covers the foliage with its stout threads so thickly that it is conspicuous for a long distance. The finest stands of *Pachycormus* were found near the divide between Punta Prieta and Bahía Los Angeles at 300 to 400 m. elevation on rusty-red volcanic clay. They here form 75 per cent of the stand of large perennials, being accompanied by *Bursera microphylla*, *Fouquieria splendens*, and *Jatropha cuneata*, with infrequent individuals of *Idria* and *Pachycereus* and no *Agave Shawii*.

The heaviest stands of *Idria* were found on high bajadas near Punta Prieta, on deep, stony volcanic clay (pl. 23). The commonest associates of *Idria* in these situations are *Pachycereus*, *Agave Shawii*, and *Yucca valida*. *Pachycormus* is infrequent in the heaviest stands of *Idria*, but is abundant on adjacent north and west slopes, where *Idria* is more poorly represented. In all the communities visually dominated by *Idria*, *Pachycormus*, *Pachycereus*, *Yucca valida*, and *Agave Shawii*, there is a discontinuous cover of shrubs from 5 to 10 dm. high, with cacti and smaller species of *Agave*, the whole forming a cover of 35 to 60 per cent. In general the cover has a uniform density on clay soils and is scattered and aggregated on granitic sandy loam.

The following list combines the records of composition and frequency for three localities within 25 km. of Punta Prieta on plains and bajadas of clay or loam.

***Idria columnaris
***Pachycereus Pringlei
***Agave Shawii
***Franseria magdalenae
***Viguiera deltoidea
***Encelia frutescens
***Agave deserti
***Opuntia clavellina
**Yucca valida
**Pachycormus discolor
**Franseria chenopodifolia
**Jatropha cinerea

**Opuntia ciribe	*Franseria camphorata
**Pedilanthus macrocarpus	Lemaireocereus Thurberi
**Larrea tridentata	Agave sobria
*Lycium californicum	Ferocactus viscainensis
*Lophocereus Schottii	Simmondsia chinensis
*Fouquieria splendens	Triteleiopsis Palmeri
*Machaerocereus gummosus	Bursera microphylla
*Prosopis juliflora var. Torreyana	Echinocereus Brandegei
*Atriplex polycarpa	Viscainoa geniculata

The Vizcaíno plain is the largest area in Baja California in which a nearly uniform vegetation extends for many kilometers in every direction. Along its inner edge, the plain is entered by a few streamways, all of which spread and disappear in a short distance. The behavior of the local drainage is indicated by bands of heavy vegetation separated by broader bands of nearly bare desert pavement at nearly the same level. At 5 to 8 km. from the edge of the plain there are few traces of the drainage from the interior.

The terraces near the beach in the northern part of the Vizcaíno plain have a low vegetation very unlike that of the interior. There are a few widely scattered wind-stunted plants of *Yucca valida*, *Machaerocereus gummosus*, and *Fouquieria peninsularis*. The commonest shrub is *Frankenia Palmeri*, and *Lycium*, *Atriplex*, *Dudleya*, and *Echinocereus maritimus* are abundant.

A few dunes are found in the northernmost part of the plain near the last of the coastal hills. All the dunes seen were very active, and their only plants were in thickets at the base of their lateral slopes. On the dunes there are none of the characteristic desert plants, but many of the dune and beach plants of northern Baja California. Among them are *Rhus integrifolia*, *Sphaeralcea axillaris*, *Helianthus niveus*, *Oenothera crassifolia*, *Hosackia nivea*, and *Abronia maritima*. Level stretches along the beach have a close sod of *Monanthochloe littoralis* or open stands of *Frankenia*, a prostrate *Lycium*, *Sesuvium portulacastrum*, *Allenrolfea occidentalis*, and *Encelia ventorum*.

The dominant plant of the Vizcaíno plain is *Yucca valida*, which forms from 60 to 80 per cent of the number of large perennials throughout the northern part of the plain. The tallest individuals are from 7 to 10 m. high. The manner of growth is such that there is no suggestion of a canopy of foliage among the trees near the observer. When an expanse of *Yucca* forest is seen from a slight elevation, it gives the impression of having an open canopy not unlike that of the dry pine barrens of the southeastern United States. This resemblance is heightened by the dark green of the leaves, a shade which is rare among desert plants. *Yucca valida* grows chiefly in close groups of 5 to 15 plants. It is erect until it reaches about half its mature height, and then begins to lean. Near the coast the trees are inclined away from the wind, but in the interior they lean and bend grotesquely in every direction. Very rarely do the individuals or groups of *Yucca valida* have the symmetrical and balanced form that is so universal in *Y. brevifolia* in the Mojave Desert.

There appear to be few places on the Vizcaíno plain where the heavy stands of *Yucca valida* extend to within 3 or 4 km. of the coast, at which distance all large plants give way to thin stands of low perennials. *Pachycereus* is relatively infrequent on the Vizcaíno plain and seldom produces branches. *Pachycormus*, *Idria*, and *Agave Shawii* are uncommon there. *Machaerocereus gummosus* is widely distributed in Baja California, but here reaches its maximum abundance. *Fouquieria peninsularis* occurs infrequently in the northern Vizcaíno Region, but is a characteristic plant of the Vizcaíno plain.

The following are the principal perennials of the Vizcaíno plain:

***Yucca valida
***Franseria magdalenae
***Lycium californicum
***Encelia frutescens
**Opuntia calmalliana
**Fouquieria peninsularis
**Viguiera deltoidea
**Jatropha cinerea
**Machaerocereus gummosus
*Atriplex sp.
*Pedilanthus macrocarpus
*Viguiera purisimae
*Euphorbia misera
*Opuntia ciribe
*Prosopis juliflora var. Torreyana
Larrea tridentata
Viscainoa geniculata
Lophocereus Schottii
Lycium Fremontii
Bursera Hindsiana
Lippia fastigiata
Pachycereus Pringlei
Triteleiopsis Palmeri
Solanum Hindsianum

The entire Vizcaíno plain lies below 100 m. elevation, and its inner edge is sharply marked by a sudden rise onto volcanic mesas. From the margin of the mesas there is a gradual rise for 10 or 15 km. to the interior plateau, lying slightly above 500 m. A strong contrast between the vegetation of the plain (pl. 26) and that of the mesas is observable from Pozo Alemán to the vicinity of San Ignacio. On the mesas there are very few large perennials, but there is a continuous stand of shrubs varying greatly in density and showing a tendency to occur in groups. *Yucca valida* is still present, but greatly reduced in size and abundance. *Pachycereus* and *Fouquieria peninsularis* are more abundant than on the plains. *Agave Shawii* and *A. deserti* are absent, but *A. sobria* is infrequently seen. *Idria* and *Pachycormus* are no longer found. Conditions more xeric than those of the plain are indicated by the occurrence of *Larrea*, *Jatropha cuneata*, *Bursera microphylla*, and *Cercidium sonorae*, and by the abundance of *Opuntia ciribe* and *O. cholla*. The coverage varies greatly, being as low as 10 per cent on very shallow soil and locally as high as 60 per cent where the shrubs are closely grouped.

The vegetation of the volcanic mesas east of the Vizcaíno plain may be summarized as follows:

**Jatropha cuneata
**Franseria magdalenae
**Opuntia cholla
**Lycium californicum
**Fouquieria peninsularis
*Encelia farinosa
*Jatropha cinerea
*Opuntia ciribe
*Machaerocereus gummosus
*Larrea tridentata

*Encelia californica
*Franseria Bryantii
Viguiera deltoidea
Atriplex polycarpa
Agave sobria
Bursera microphylla
Yucca valida
Echinocereus Brandegei
Pedilanthus macrocarpus
Opuntia invicta
Bursera Hindsiana
Pithecellobium confine
Mammillaria sp.
Cordia parvifolia
Bebbia juncea
Asclepias subulata
Hibiscus denudatus
Petalonyx linearis
Stillingia linearifolia

Magdalena Region

(Arbocrassicaulescent Desert. Lysiloma-Machaerocereus Region)

The Magdalena Region is the southernmost part of the Sonoran Desert, extending 3° of longitude (350 km.) farther south than the mainland part. The eastern boundary is formed by a more continuous series of higher mountains than is the case in the Vizcaíno Region. The northern half of the region, between San Ignacio and Comondú, is an intricate field of volcanic hills and mesas, with a narrow, sandy coastal plain. Much of the area is occupied by long tongues of volcanic eruptives falling at a uniform gradient from the central series of extinct cones. The volcanic tongues are uniformly nearly level in transverse section, with rocky surface and shallow soil, and are steep on the sides. Between the tongues are narrow barrancas with soil and local seepages of water. Comondú, San Miguel, and Purísima are located in the bottoms of large valleys of this type, in which a constant water supply is available.

South of Comondú the coastal plain widens gradually into the Magdalena Plain, which occupies half the width of the peninsula at latitude 25° N. and then tapers southward to the latitude of La Paz (24° 10′ N.). Offshore at the broadest part of the Magdalena Plain are the islands Magdalena and Santa Margarita, and Cabo San Lazaro, at the end of a long barrier island. These three islands are occupied by low hills, but there are no hills on the Magdalena Plain. It is obvious that the plain has been built by the deposition of outwash material from the Sierra de la Giganta, and the presence of the hilly islands suggests that deposition began in a shallow bay. Innumerable streamways drain the west face of Sierra de la Giganta, and, according to the most detailed maps of Baja California, all gather into four large arroyos which debouch into the coastal lagoons. Examination of the plain after the very rainy winter of 1935 showed clear evidence that part of the mountain drainage reaches playas from which it does not escape. At that time all the large playas and many of the small ones were shallow lakes, and some of them were so thickly covered with plants that they resembled meadows.

Not only are large playas common, but very small ones (*playitas*) are extremely abundant. Away from sandy soil, a single hectare commonly has from twenty to fifty small bare depressions from 5 to 15 m. in diameter (see pl. 29). Their

presence explains the lack of small drainageways for local runoff on the floor of the plain. North of Venancio and the Arroyo Flor de Malva there are no small stones on the soil surface in any situations, and even in the largest arroyos stones are few. The prevailing color of the soil is light gray. At the north end of the plain there are several large areas of very light gray volcanic ash. Along the coastal margin of the plain there is much sandy soil, and there are dunes of moderate size at several localities.

In the inland settlements of the Magdalena Region the residents state that there are occasional frosts as far south as Purísima, but only very light and infrequent ones farther south. The mean annual rainfall is 202 mm. at La Paz and is probably of similar amount throughout the lowlands of southern Baja California. On the Pacific coast the rains are almost wholly in the late winter. On the Gulf coast and throughout the interior there are summer thunderstorms as well as gentle winter rains. Recent periods of 3 to 5 years without rain were reported at several localities in 1935. On the Magdalena Plain there is some morning fog in all months, but it is most persistent in April and May. At Comondú and San Miguel there is no fog from the Pacific, but it sometimes spreads inland from the Gulf of California.

Northern Magdalena Region. North of Comondú, volcanic mesas and slopes form the prevailing surface. There are extensive malpais fields with scattered pockets of soil, and also areas of thin but continuous soil strewn with small stones. The surface has undergone little change from erosion, but has many structural rifts and barrancas. The vegetation of the malpais and the thin soil of the mesas is open, irregular, and xeric, closely resembling that of the area east of the Vizcaíno plain. Some of the cliffs and barranca walls apparently receive no seepage of water and are thinly covered or naked. Other steep slopes which have soil, seepage, and northern aspect are heavily clothed with communities in which many of the thorn forest species of the Cape Region make their first appearance and mingle with desert plants. In the largest barrancas the streamways and small shelves of alluvial soil support a heavy mesic vegetation in which there are few desert plants.

South of Purísima and around the north end of the Magdalena Plain the rainfall is evidently very low. The vegetation here is extremely open and almost wholly made up of species characteristic of the very desert areas of Baja California and Sonora. In the most xeric habitats of the northern Magdalena Region there are only a few prominent plants which do not extend north of San Ignacio. The most favorable habitats are not dominated by any one plant, but by an assemblage which is largely made up of plants near their northern limits.

The vegetation of the volcanic mesas varies in its height and density. On the very rough malpais, plants are very irregularly distributed and vary from 1 to 4 m. in height. Rough malpais is very difficult to traverse, as the only places where the footing is good are densely covered with shrubs. On uniform surfaces the spacing is more even, but the stature is similar.

The landscapes of the Magdalena Region are less striking than those of the Vizcaíno Region. This difference is due primarily to the absence of *Idria* and *Pachycormus* and the infrequency and poor development of *Pachycereus* and all the species of *Yucca* and *Agave*. Also there is a greater uniformity in the life forms, with microphyllous trees and shrubs taking the dominant place. On the volcanic mesas cacti are relatively infrequent, with *Lophocereus Schottii*, *Machaerocereus gummosus*, and other tall forms very infrequent. The cylindropuntias are very irregular in occurrence, forming open colonies in one spot and being absent over large areas. The platyopuntias, which are very uncommon in the Vizcaíno Region, are abundant in many parts of the Magdalena Region.

In the hills west of San Miguel, where there is little malpais, the vegetation resembles that of the Gulf coast of Sonora more closely than does that of any other place in Baja California. The coverage is rarely above 5 to 10 per cent. The similarity is due to several dominants which these areas have in common, and to the close resemblance between some of the specifically distinct dominants. In the following list of characteristic species the ones also found in Sonora are marked "S," and after those with close analogues in Sonora the name of the Sonoran plant is given in parentheses.

***Larrea tridentata	S
***Jatropha cuneata	S
***Opuntia cholla	(Opuntia fulgida)
***Atriplex polycarpa	S
**Jatropha cinerea	S
**Lophocereus Schottii	S
**Machaerocereus gummosus	(Rathbunia alamosensis)
*Bursera microphylla	S
*Fouquieria peninsularis	(Fouquieria splendens)
*Lycium brevipes	(Lycium Fremontii)
*Pachycereus Pringlei	(Carnegiea gigantea)
Lemaireocereus Thurberi	S
Acacia Brandegeana	(Acacia occidentalis)
Cercidium sonorae	S
Ditaxis lanceolata	S
Caesalpinia arenosa	(Caesalpinia pumila)
Fagonia californica	S
Encelia farinosa	S
Krameria paucifolia	(Krameria Grayi)

The barrancas which drain the volcanic mesas have sharp crests, and it is rarely that they are joined by tributary barrancas or receive much lateral drainage. The upper walls of the barrancas are steep, and the only tree suited to gain foothold there is the semiscandent *Ficus Palmeri*. When the descent from the crest of the barranca is more gradual, there is a heavy stand of shrubs with scattered trees and columnar cacti (pl. 28). Such vegetation is very uneven in the distribution of its components. Small colonies may be found of shrubs which

are uncommon elsewhere. The Opuntias and smaller cacti are sporadic in occurrence. Trees are very widely spaced except where local conditions are specially favorable. In the rich composition and irregular distribution of their vegetation the barrancas are in sharp contrast with the level mesa above, and bear a strong resemblance to similar situations in the Foothills of Sonora.

In the following list are mentioned only the most common of the many species found in the barrancas, with no attempt to indicate their relative abundance. The first seven are the most conspicuous ones.

Pachycereus Pringlei
Fouquieria peninsularis
Lemaireocereus Thurberi
Bursera odorata
Lysiloma candida
Prosopis Palmeri
Opuntia comonduensis
Viguiera deltoidea
Acacia Brandegeana
Colubrina glabra
Berginia virgata
Franseria ambrosioides
Ruellia californica
Jatropha cinerea
Opuntia alcahes
Brickellia Coulteri
Schoepfia californica
Randia megacarpa
Carlowrightia californica
Viguiera tomentosa
Opuntia sp. (platyopuntia)
Pithecellobium confine

The large barrancas, or valleys, differ from the smaller ones in having much more xeric conditions on their slopes and much more favorable moisture conditions along the floor. Dense jungles of trees and large shrubs occupy all the uncultivated areas in the valley of Comondú. The number of small perennials is large, and palustrine and aquatic plants find a few favorable habitats. The dominant trees are *Cercidium peninsulare*, *Prosopis juliflora* var. *Torreyana*. *P. Palmeri*, *Lysiloma candida*, and *Parkinsonia aculeata*, above which rise groups of *Washingtonia robusta*. The shrubbery is chiefly *Tecoma stans*, *Viguiera tomentosa*, *Vallesia glabra*, *Alvordia angusta*, *Euphorbia Xanti*, and *Berginia Palmeri*. Farther north in Baja California and Sonora the well watered habitats of this character are not without a few xeric plants, but here there are none.

The coastal plain west of Purísima and Comondú and north of the Magdalena Plain has a light brownish gray sandy soil, with more open and xeric vegetation than any occurring farther south on the Pacific coast. Just inside the coastal lagoons there is a belt of active dunes from 2 to 3 km. in width. On the sandy plains which extend inland from the dunes the coverage is about 5 to 10 per cent. Sparingly branched plants of *Pachycereus* are the most conspicuous element, and trees are very widely spaced. This simple vegetation is composed as follows:

***Opuntia cholla
***Franseria magdalenae
***Encelia farinosa
**Pachycereus Pringlei
**Jatropha cinerea
**Fouquieria peninsularis
*Euphorbia magdalenae
*Larrea tridentata
Machaerocereus gummosus
Opuntia tesajo
Solanum Hindsianum
Bursera Hindsiana

Two unusual plants are confined to this immediate vicinity, *Euphorbia magdalenae* and *Machaerocereus eruca*. The former is a very compact shrub with slender green stems bearing a few short-lived leaves on the youngest shoots. It resembles *Euphorbia colletioides* of Sonora in every respect except its dense habit of growth. *Machaerocereus eruca* is in effect a stout columnar cactus which has adopted a prostrate habit of growth. The trunks are rooted throughout their length, and the oldest parts gradually die as the plant slowly advances in the usually straight course determined by the growing tip. The slightly elevated position of the youngest 20 or 30 cm. of the stem has led Goldman to liken the colonies of *Machaerocereus* to groups of huge catepillars (for illustration see Goldman, 1916, pl. 127).

In several small areas on the inner edge of the northern end of the Magdalena Plain the soil is a light gray, impalpably fine volcanic ash. Nothing is known about the behavior of such a surface under light or heavy rain, nor about the infiltration or retention of water. Much of the surface is bare of perennials. When seen in March, after heavy rains, most of the ash was bare, but parts of it were covered with *Plantago*. The only perennials found on it were *Franseria magdalenae*, *Encelia farinosa*, and *Opuntia cholla*.

Southern Magdalena Region. The Magdalena Plain from San Domingo to Venancio, a distance of 180 km., is very uniform in its physical features and monotonous in its vegetation (pl. 29). There are no changes in level until the gradual rise toward Sierra de la Giganta is reached, about halfway across the peninsula. There are very few arroyos and no small streamways. The only interruptions to the uniformity of the vegetation are due to the innumerable playitas and the frequent large playas, some of which are meadows or lakes in wet seasons.

The profile of the vegetation is irregular, being formed by either *Prosopis* or *Lycium* and by the projecting tops of *Pachycereus*. There are no tall plants of this cactus, but many massive ones which have branched just above the ground. Other cacti, *Lemaireocereus*, *Lophocereus*, *Machaerocereus gummosus*, and *Opuntia cholla*, are very abundant, but are outnumbered by the microphyllous trees and shrubs. The absence of perennials from the playitas does much to make the profile of the vegetation irregular. The coverage varies from about 40 to 80 or 90 per cent, but the more open type covers the greatest area. The minimal area is small, as there are few large perennials and these are of infrequent occurrence.

The following conspectus of the vegetation is based on four nearly identical determinations between Médano Blanco and Venancio:

***Prosopis juliflora var. Torreyana
***Lycium brevipes
***Opuntia cholla
**Fouquieria peninsularis
**Machaerocereus gummosus
**Pachycereus Pringlei
**Euphorbia californica
*Lemaireocereus Thurberi
*Franseria Bryantii
*Lycium Andersonii
*Lophocereus Schottii
*Opuntia tesajo
*Prosopis Palmeri
*Franseria magdalenae

Cercidium floridum
Jatropha cinerea
Hyptis laniflora
Maytenus phyllanthoides
Encelia farinosa

Three small arroyos were observed in the Magdalena Plain which were bordered by narrow strips of recently dissected ground. In these situations several xeric perennials were found which are uncommon elsewhere on the Plain, including *Koeberlinia spinosa*, *Olneya tesota*, *Jatropha cuneata*, *Bursera odorata*, and *Simmondsia chinensis*. In reverse of the usual case, the margins of these arroyos appear to be drier than the surrounding surface, doubtless owing to desiccation of the soil from the dissected surfaces.

South of El Refugio there is a large area in which the vegetation is more xeric than elsewhere. *Prosopis* and *Lycium* are infrequent, and the dominant plants are *Larrea tridentata*, *Opuntia cholla*, *Fouquieria peninsularis*, *Franseria magdalenae*, *Jatropha cuneata*, and *Bursera microphylla*, accompanied by other plants in the list above. Small areas of volcanic ash in this region are covered by open, nearly pure stands of *Larrea*.

Between the sandy region around Médano Blanco on the north and the Arroyo Flor de Malva on the south there are many large playas and seasonal meadows. In some cases the floor of the playa is bare and its margin covered with herbaceous perennials and annuals. In other cases the entire playa is heavily covered with grasses, sedges, and herbaceous plants. The composition in the seasonal meadows is rich and varies from playa to playa. The genera represented are those common to moist soils throughout Baja California, Sonora, and Sinaloa, but many of the species are endemic to southern Baja California.

A few of the commonest plants observed in a meadow 9 km. south of Querétaro are:

Leptochloa viscida
Eragrostis cilianensis
Eragrostis diffusa
Cyperus aristatus
Mecardonia exilis
Vicia exigua
Lythrum Bryantii
Verbena bajacalifornica
Eryngium nasturtiifolium
Castilleja Bryantii
Coreocarpus parthenioides
Rumex conglomeratus
Marsilea Fournieri

South of the Arroyo Flor de Malva the coastal plain narrows to a width of a few kilometers, and gentle rocky slopes run down nearly to the sea. The foundation of this area is limestone, as shown in cliffs 30 m. high along the left bank of the arroyo. Volcanic intrusives also occur and contribute coarse angular material, with which are interspersed many waterworn pebbles.

The vegetation of the southernmost tip of the Magdalena Region is dense, low, and poor in large perennials. *Yucca valida* is prominent in some places, particularly in depressions, but is only 2 to 3 m. in height. *Pachycereus* is rare. *Fouquieria peninsularis* is abundant but rarely more than 2.5 m. high. The pre-

vailing shrubs are *Lycium*, *Encelia*, *Simmondsia*, and *Atamisquea*. Near the coast a uniformly gray color is given the landscape by the abundance of the lichen *Rocella*, which covers every branch and twig.

South of Arroyo Flor de Malva there are no coastal lagoons, and a narrow belt of sand dunes lies just inside the beach. Much of the dune surface is very active and bare of plants. Stabilization appears to proceed rapidly, however, when once begun, and to be aided by an unusually large number of species. The mature slopes are covered by dense thickets of *Maytenus phyllanthoides*, *Stegnosperma halimifolium*, *Caesalpinia arenosa*, *Simmondsia chinensis*, and *Lycium brevipes*.

To travel east from the inner edge of the Magdalena Plain toward the slopes of Sierra de la Giganta is to pass rapidly from desert into the Cape thorn forest. The coverage in the lower foothills is 60 to 80 per cent, which is about the same that is found in the sandy lowland parts of the Cape Region. Certain spots are more open and others are very dense. Small trees become rapidly more abundant, and so many of the shrubs are over 2 m. high that it is not possible to see very far through the vegetation. Cacti, yuccas, and *Fouquieria* are still abundant, and the trees are nearly all microphyllous deciduous types. It is manifest that the environment is still an arid one, but one in which the aridity is greatly ameliorated. The average height of the trees is about 5 to 6 m., but the canopy is irregular. There is no layering, and the open branching and sparse foliage of the trees allow strong light to reach the floor of the forest.

The following list of perennials characteristic of the inner edge of the Magdalena Region is based on examination of it at the northern and southern ends. Though many of the same species are found at these extremities, there is some difference in their relative abundance, and a few are found only at the southern end.

Jatropha cinerea
Lysiloma divaricata
Fouquieria peninsularis
Bursera microphylla
Prosopis Palmeri
Randia Thurberi
Lophocereus Schottii
Cyrtocarpa edulis
Bourreria sonorae
Opuntia cholla
Tecoma stans
Bursera odorata
Euphorbia Xanti
Esenbeckia flava
Haematoxylon brasiletto
Yucca valida
Cercidium peninsulare
Forchammeria Watsoni
Melochia pyramidata
Pithecellobium confine
Encelia farinosa
Hyptis laniflora
Larrea tridentata
Lemaireocereus Thurberi
Bursera filicifolia
Ruellia peninsularis
Mimosa laxiflora
Colubrina glabra

4

Ephemeral Herbaceous Vegetation

IN THE SKETCH of the vegetation of the Sonoran Desert in the preceding chapter, attention was confined to perennial plants. The short-lived herbaceous plants, however, form about half the flora and also play a conspicuous role in the vegetation in their appropriate seasons. For several reasons it has seemed better to give separate treatment to the herbs, which are here designated "ephemerals" rather than "annuals" because their life span rarely fills the entire growing season as measured by frostless temperatures.

The desert environment offers particular advantages to the short-lived plant. The restriction of its vegetative activity to brief moist periods almost completely relieves the ephemeral plant from the difficulties of water supply which beset the perennial. By speed of germination, rapidity of growth, and early flowering and maturity during favorable periods the ephemeral escapes the most potent one of the conditions controlling the life and ecological behavior of desert plants. Also the large expanses of bare ground assure ephemerals ample space and little competition with established plants.

The appearance of ephemerals follows periods of moderate or heavy rain, whether this occurs regularly in the cool months or the hot months or at rare and sporadic intervals. There is a minimum of rainfall below which the ephemerals do not appear, but there is no maximum which is deterrent to them. It follows that the geographic distribution of the species of ephemerals is determined by the seasonal incidence of the moist periods. It is scarcely affected by the annual or seasonal totals of rain, by the length and severity of drought periods, by the high maximum temperatures of summer, or by the freezing temperatures of winter. The environment is much more simple for the ephemeral than it is for the perennial. This is shown by the fact that the ephemeral vegetation of the Sonoran Desert falls into a smaller number of regional categories than does the perennial vegetation.

The most favorable local habitats for ephemerals are merely those affording an abundant and briefly sustained moisture supply. The character of the soil is of little importance aside from its penetrability and retentiveness. The depth, structure, and mineralogical origin of soils, all so important to perennials, mean little to the ephemeral. Sand, however, is a particularly favorable soil for the ephemerals of the cool season, because of the deep infiltration of moisture and the rapid warming of the surface early in the season and early in the day. In any part of the Sonoran Desert it would be difficult to make a local differentiation of habitats solely on the basis of the short-lived herbaceous plants. Their local distribution is determined by the moisture of the soil, the character of the soil

surface, and the shade of perennials. The character of the surface is important in several respects. On sand the wind-blown seeds are covered, held, and left at a favorable depth for germination. In general the crop of ephemerals is much more evenly distributed over a sandy soil than over any other. On a hard, smooth surface with little vegetation there is rarely a thick crop of ephemerals, as their seeds are either washed away or blown away. A slight depression in such a surface is usually thickly colonized. On undisturbed desert pavement the chances for lodgment of seeds are also poor, and few germinations take place there (see pl. 1). On a surface with small projecting stones there is a light or moderately heavy crop. On slopes covered with large stones the ephemerals are abundant but localized. In the shade of perennial plants the ephemerals are larger and more numerous than in the open. Under low, spreading shrubs the crop is larger than under trees. The larger numbers are due to the arresting of wind-borne seeds by the shrub and its dead undergrowth; the larger size, to conservation of moisture by the shade of the shrub and to the shade effect on the ephemeral (see pl. 30).

In slight depressions or on benches where conditions have been favorable for the accumulation of seeds at the end of the active season, the number of seedling ephemerals may be very great. On a slightly shaded level area of deep, moist clay near Tucson, 1200 seedlings of *Plantago* were counted on a square meter. It is characteristic of such colonies that they are composed of a single species or have one species greatly predominant. This is probably due to the depositing of the seeds by the runoff of a rain which happened to occur just when the seed crop of the predominant species was ripe for distribution. In such heavy stands competition is great, and the vast majority of the seedlings perish. Dense stands of ephemerals are commonest on flood plains and in other situations with level alluvial soil, a fact which points to flood water as the agent in their distribution. Such stands are particularly characteristic of *Monolepis Nuttalliana*, *Pectis papposa*, *Plantago insularis*, and *Amaranthus Palmeri*. On gentle slopes and other surfaces covered with coarse lag gravel the ephemerals are more widely spaced and numerous species more evenly intermingled.

A feature which lends particular interest to the ephemeral plants of the Sonoran Desert is the existence of two distinct groups of species which are respectively confined in their appearance to the warm and the cold rainy periods. The seasonal distribution of rainfall is controlled by broad climatic conditions and appears to have undergone little change in this region, at least since early Pliocene time, whatever fluctuations may have taken place in the amount.

The Pacific coast of Baja California, like that of California, is visited by rain only in the winter and early spring. The winter rains extend eastward across Arizona and Sonora, diminishing in amount. Summer rains are general along the eastern edge of the Sonoran Desert, diminishing toward southern Baja California, northwestern Sonora, and western Arizona, and only infrequently visiting southeastern California. Because of the overlapping of the winter and summer rainfall areas, a wide belt of the Sonoran Desert receives biseasonal precipitation. In the vicinity of Tucson the average amounts of summer and winter rain are nearly

equal. South of the international boundary, the winter rain diminishes in amount and in percentage of the annual total. These features of rainfall distribution are critical in controlling the ranges of the two groups of ephemerals.

The fact has long been known, and confirmed by several workers, that the restriction of the two groups of ephemerals to their respective seasons is dependent on the optimum temperature for germination of their seeds. For winter ephemerals the optimum is between 60° and 65° F., and for summer ephemerals between 80° and 90° F. The optimum differs slightly for the different species that have been tested in each group, and for nearly all species in either group germination is fairly prompt and complete within a range of about 5° to 8° above or below the optimum.

The narrow margin of 5° to 10° between the highest possible germination temperature for winter ephemerals and the lowest for summer ephemerals is sufficient for the sharp seasonal separation of the two groups, with certain exceptions to be noted later. In winter the seeds of summer ephemerals remain dormant under favorable conditions of soil moisture, and likewise in summer the seeds of winter ephemerals lie in a moist soil without germinating.

Little is known about the length of the period for which viability is retained by the seeds of desert ephemerals. It has been observed that an exceptionally favorable season will bring forth large crops of species that have been uncommon for ten to fifteen years. Also the relative abundance from year to year of the regularly recurring species does not bear a constant relation to the extent of the population and seed crop of the immediately preceding two or three years.

With their vegetative activity confined to a moist period, the ephemerals are chiefly mesomorphic in foliage. There are great differences among them, however, in habit, in normal limits of height, in manner of branching, and in the size, thickness, surface, and manner of display of the leaves.

Certain ephemerals have a narrow range of variation in height, as *Cryptantha*, *Pectocarya*, *Pectis*, and many species of *Eriogonum* and *Gilia*, whereas others vary from a few centimeters to 2 or 3 m. in height, as *Sphaeralcea Coulteri* and *Amaranthus Palmeri*. Height and bulk are chiefly determined by the amount of soil moisture available during the growing period, and, in the case of winter ephemerals, by the number of warm and sunny days following the rainy periods. Individuals of the same species may come to maturity at a height of 1 cm. with a single flower or may grow to a height of 2 or 3 dm., bearing hundreds of flowers. Such divergence of behavior is due to the amount of precipitation. A recurrence of rain after a short dry period frequently causes a renewal of growth in small plants and may result in a second crop of flowers. The duration of life of the ephemeral is commonly limited to 6 or 8 weeks, but may be prolonged by extraseasonal rains. A few quasi-perennial species germinate in the winter and, with unusually late spring rains, may persist into the summer.

Economy of material in development of stems and exposure of leaf surface has obviously been a factor in the development of the ephemerals. In spite of their lives' being brief and led in the most favorable season, they are nevertheless

desert plants, subjected to strong insolation and dependent on a short-lived and precarious water supply.

Very few species have stems which are thick or provided with a strong development of mechanical tissue. On the other hand, there are numerous prostrate forms, as *Hosackia*, *Pectis*, *Achyronychia*, *Tidestromia*, *Calyptridium*, *Bowlesia*, and many species of *Euphorbia*. In an even larger number of genera there are many semiprocumbent plants, in which the lowest third or half of the stem rests on the ground, as *Nama*, *Gilia*, *Cryptantha*, *Monoptilon*, and *Eriophyllum*. In the erect species the stem is usually slender and in some cases very slender, as in *Nemacladus*, *Eremocarya micrantha*, *Parietaria*, *Greenella*, and many others. The stoutest stems are found in certain species of *Oenothera* and *Mentzelia* and in *Dicoria*, *Lupinus*, *Streptanthus*, *Cirsium*, *Martynia*, and *Helianthus*. A curious type of greatly inflated hollow stem is found in *Eriogonum inflatum;* in the Mojave Desert it occurs in *Caulanthus inflatus* and is weakly developed in *Oenothera decorticans* var. *condensata*. The most ingenious proponents of adaptational suggestions have been unable to ascribe any survival value to the inflated stems, and there is no obvious physiological explanation for their development.

A very common type of ephemeral is one in which a small rosette of prostrate or nearly prostrate leaves is formed, from which one or more shoots arise. The shoots may bear a few leaves, diminishing in size toward the top, may bear small bracts, or may be naked. The formation of basal rosettes is characteristic of many species in *Oenothera*, *Eriogonum*, *Chorizanthe*, *Chaenactis*, *Draba*, and *Malacothrix*, and in *Salvia columbariae* and others. The rosette of leaves usually dies before the seeds mature. The chlorophyll-bearing tissue of the stems and bracts is capable of making some contribution toward the filling of the seeds. In several species of *Eriogonum*, notably *E. deflexum* and *E. polycladon*, the stems are richly branched and remain alive for several weeks after all other ephemerals have died. In these plants the seed crop is much larger than in most of the other ephemerals.

Some of the most aggressive and drought-resistant herbs remain alive and more or less active after the majority of ephemerals have matured and died. The line of demarcation between ephemerals and herbaceous perennials is not sharp, and, indeed, not constant in the same species. Some of the perennating species are very dependent on extraseasonal rains for their survival. Others, like the species of *Eriogonum* mentioned above, lose their rosette of mesic leaves and persist as leafless green-stemmed plants, suggesting miniature trees of *Canotia* or *Holacantha*. Among the summer Compositae there are several species that germinate and grow quickly but bloom less promptly than other ephemerals and often persist to the second year (*Verbesina encelioides*, *Xanthium pennsylvanicum*, *Helianthus petiolaris*).

The disturbed conditions and supplementary water supply on roadsides, canal banks, and fields give an opportunity for perennation to several native and introduced plants that are strictly ephemeral in natural situations.

A few ephemerals may be regarded as recent derivatives from perennial races, in which continued subjection to long drought periods has fixed the ephemeral

habit. This suggestion may apply to *Cassia Covesii* (still often truly perennial), *Atriplex elegans*, *A. Wrightii*, and *Haplopappus gracilis*.

Very few ephemerals have leaves larger than 4 sq. cm. (*Amsinckia tessellata*, *Datura*), and in the great majority the leaves are less than 1 sq. cm. in area. Many anatomical features found in the leaves of desert perennials are regarded, with more or less evidence, as concerned in protection from excessive insolation or water loss. The leaves of ephemerals are fully as diversified as those of perennials, including a highly mesic type (*Parietaria floridana*, *Bowlesia incana*), a less mesic type (*Phacelia crenulata*, *Boerhaavia erecta*), lightly cutinized ones (*Hosackia brachycarpa*, *Eremalche rotundifolia*), and still others with heavy epidermis and cuticle (*Perezia nana*, *Chorizanthe rigida*). Entire or slightly cut leaves are rare outside the most mesic types. In nearly all leaves with an area of 1 sq. cm. or more, the blade is divided or deeply dissected (*Phacelia* spp., *Lepidium* spp., *Astragalus* spp.). In the much larger group of ephemerals with leaves less than 1 sq. cm. in area, there are many with narrow entire leaves (*Plantago*, *Platystemon*), or with leaves which are very short as well as narrow (*Pectis* spp., *Pectocarya* spp.).

A long series of ephemerals might be cited in which the leaves have a gray color due to air-filled epidermal cells (*Tidestromia*, *Dicoria*), close pubescence (*Geraea canescens*, *Stylocline micropoides*), or long wool (*Eriophyllum lanosum*, *Trichoptilium incisum*). Succulent leaves are found in a few species (*Portulaca pilosa*), and slightly succulent ones in others (*Calandrinia ciliata*, *Tillaea erecta*). Leaves beset with oil glands are found in a number of ephemerals, especially in the Compositae (*Dyssodia concinna*, *Pectis papposa*).

A striking development of the ephemeral has given rise to a series of plants in which the stem is erect or semierect but very slender, much branched, and either leafless or sparsely covered with very small leaves or bracts. These forms, which may be appropriately called "shadowless plants," expend the minimum amount of material and expose a very small photosynthetic and transpirational surface. Their seeds are very small and their seedlings poorly supplied with parental material for their earliest growth. Common examples of the shadowless plants are *Nemacladus ramosissimus*, *Euphorbia revoluta*, *Mollugo cerviana*, *Linanthus aureus*, *L. dianthiflorus*, and *Houstonia asperuloides*. Further examples are supplied by several species of *Eriogonum* in the mature phase of their development.

Winter Ephemerals

Geographic Distribution of Winter Ephemerals

In southern California the native herbaceous plants are perforce limited to the winter and early spring, since the summer is rainless. The number of "annuals" credited to this area in Munz's *Flora of southern California* is 965, including 765 species and 200 varieties and forms, and excluding a number of species which sometimes persist beyond their first year. Of this number, 358 species and 111

varieties and forms are restricted to the coast, and 407 species and 89 varieties and forms are found in the Mojave Desert and in the arm of the Sonoran Desert which extends into southeastern California and is often ambiguously called the "Colorado Desert."

The Mojave Desert is particularly rich in ephemerals, probably having 250 species and varieties. Of this number more than one-third are confined to the Mojave Desert, while others extend north into the Great Basin or are found also in the Sonoran Desert. The greatest number of species and the greatest abundance of individuals are found along the elevated southern and western edge of the Mojave Desert. To the north and east of this belt there is a reduction in both species and numbers.

On the Pacific coast of Baja California the ephemerals are also restricted to the winter. In the chaparral of northwestern Baja California the ephemerals correspond closely to those of coastal southern California in both floristic and ecological respects. South of the latitude of Rosario the relation to the northern coastal region becomes much less. The Pacific coast has obviously been the center of development of the ephemerals which respond to a cool, moist period. If the ephemerals of the rich flora of the Mojave Desert are followed eastward, their numbers are found to diminish rapidly through the Colorado Valley and the Arizona Upland. If they are followed south along the Gulf coast, they are found again to diminish on both sides of the Gulf. Both to the east and to the south a few species are added to the group which are not found in the Mojave Desert.

Winter Ephemerals of Baja California

In the desert parts of Baja California there is a rich display of ephemerals on suitable surfaces for several weeks following heavy winter rains. In the very rainy spring of 1935 the most favorable localities were heavily covered with a flourishing growth of ephemerals, from which was obtained most of the information about them in the following paragraphs. In the dry spring of 1934 scarcely 100 individuals of this type of plant were seen between Rosario and Bahía Concepción. The rainfall records indicate that there must be from four to seven such years in every decade.

The relative abundance of the common ephemerals varies greatly. Nearly pure stands of a single species are often seen, but are not usually more than 10 to 15 m. in diameter. Stands in which from 3 to 5 species dominate are more common and larger. Stands with 10 to 15 species are common on the heaviest soils in well watered locations. In 1935 the inner edge of the Vizcaíno plain was covered with a stand of 15 to 20 species so heavily that little bare ground was left exposed (pl. 26). The genera most abundantly represented are *Plantago*, *Cryptantha*, *Perityle*, *Eriogonum*, *Tillaea*, *Lepidium*, *Oenothera*, *Hosackia*, and *Phacelia*. Grasses are conspicuously infrequent and limited to open representation of *Festuca octoflora* on sandy soil and somewhat more abundant occurrence of *Muhlenbergia microsperma* on heavier soils.

The ephemeral flora is like the perennial in changing gradually from north

to south, and in showing differences between the northeastern coast and the central and Pacific coast sections, a strong relationship to the Lower Colorado Valley region, and some endemism. The coastal ephemerals of southern California are poorly represented south of the desert-chaparral transition. A very few summer ephemerals of Arizona and Sonora have been found in the winter in central and southern Baja California (*Pectis papposa*, *Bouteloua aristidoides*, *Physalis pubescens*, *Parthenice mollis*). In southern Baja California, on the Gulf coast, the dead remains of unidentifiable species of *Boerhaavia* were found in the spring, indicating the existence of at least a few summer ephemerals where there are occasional summer rains.

The total number of ephemerals native to Baja California is probably between 400 and 500 species, or slightly greater than the number in the desert areas of California. The following list of 114 species includes those that were most abundant or most widely distributed in the spring of 1935. In order to show something of regional differences, the species seen only on the northern Gulf coast are indicated by (G) and those seen only south of San Ignacio by (S). The species which also occur on the coast or desert of California, or the Sonoran Desert in Arizona or Sonora, are so designated. Names followed by "BC" indicate species which are endemic to Baja California so far as known.

Festuca octoflora	Cal. coast and desert; Ariz.
Bouteloua annua (S)	BC
Muhlenbergia microsperma	Cal. coast and desert; Ariz.
Bouteloua aristidoides	Cal. desert; Ariz.
Cenchrus Palmeri	BC
Cyperus aristatus var. inflexus	Cal. coast and desert; Ariz.
Parietaria floridana	Cal. coast and desert; Ariz.
Eriogonum scalare	BC
Eriogonum angulosum	Cal. desert; Ariz.
Eriogonum reniforme (G)	Cal. desert; Ariz.
Chorizanthe flava	BC
Aphanisma blitoides	Cal. coast
Amaranthus lepturus	BC
Boerhaavia intermedia	Cal. desert; Ariz.
Mirabilis oligantha	BC
Abronia gracilis	BC
Nemacaulis denudata	Cal. coast and desert
Atriplex elegans	Cal. desert; Ariz.
Pterostegia drymarioides	Cal. coast and desert; Ariz.
Drymaria holosteoides (S)	BC
Drymaria viscosa	BC
Achyronychia Cooperi (G)	Cal. desert; Ariz.
Loeflingia squarrosa	Cal. coast
Eschscholtzia minutiflora	Cal. desert; Ariz.
Dryopetalon Palmeri	BC
Lepidium lasiocarpum	Cal. coast and desert; Ariz.

Thelypodium lasiophyllum	Cal. coast and desert
Dithyraea californica	Cal. desert; Ariz.
Sibara laxa	BC
Lyrocarpa Xanti (S)	BC
Lyrocarpa Coulteri var. Palmeri	BC
Wislizenia refracta	BC
Oligomeris linifolia	Cal. coast and desert; Ariz.
Tillaea erecta	Cal. coast; Ariz.
Hosackia humilis	Cal. desert; Ariz.
Hosackia nivea	BC
Hosackia tomentella	Cal. desert; Ariz.
Lupinus sparsiflorus (G)	Cal. desert; Ariz.
Astragalus insularis	Cal. desert
Dalea vetula	BC
Dalea peninsularis	BC
Dalea mollis subsp. pilosa	BC
Petalostemon evanescens	BC
Cassia confinis	BC
Vicia exigua	Cal. coast; Ariz.
Polygala desertorum	BC
Ditaxis serrata	Cal. desert; Ariz.
Stillingia linearifolia	Cal. desert; Ariz.
Euphorbia polycarpa	Cal. coast and desert; Ariz.
Euphorbia Pondii	BC
Euphorbia eriantha	Cal. desert; Ariz.
Euphorbia heterocarpa var. eriocarpa	BC
Cardiospermum corindum	Son.
Sphaeralcea axillaris	BC
Sphaeralcea Orcuttii	Cal. desert; Ariz.
Sphaeralcea Coulteri	Cal. desert; Ariz.
Sphaeralcea Hainesii (G)	BC
Mentzelia adhaerens (G)	Son.
Mentzelia albicaulis (G)	Cal. desert; Ariz.
Lythrum Bryantii (S)	BC
Oenothera angelorum	BC
Oenothera clavaeformis vars. (G)	Cal. desert; Ariz.
Oenothera deltoides (G)	Cal. desert; Ariz.
Daucus pusillus	Cal. desert; Ariz.
Linanthus Jonesii	BC
Nemophila Menziesii var. integrifolia	Cal. coast and desert
Nama Coulteri	BC
Phacelia distans	Cal. coast and desert; Ariz.
Phacelia crenulata (G)	Cal. desert; Ariz.
Amsinckia tesselata	Cal. coast and desert; Ariz.
Pectocarya recurvata	Cal. desert; Ariz.
Pectocarya peninsularis	BC
Cryptantha maritima	Cal. coast and desert
Cryptantha angelica	BC

Cryptantha fastigiata	BC
Cryptantha angustifolia (G)	Cal. desert; Ariz.
Cryptantha echinosepala	BC
Cryptantha Grayi	BC
Verbena bajacalifornica (S)	BC
Verbena Shrevei (S)	BC
Salvia similis	BC
Stachys tenerrima	BC
Nicotiana Clevelandii	Cal. coast and desert; Ariz.
Nicotiana trigonophylla	Cal.; Ariz.
Mohavea confertiflora (G)	Cal. desert; Ariz.
Antirrhinum cyathiferum	Ariz. (one locality)
Mecardonia exilis	BC
Castilleja Bryantii (S)	BC
Martynia altheaefolia	Cal. desert; Ariz.
Plantago insularis	Cal. coast
Plantago fastigiata	Cal. desert; Ariz.
Houstonia brevipes (G)	BC
Nemacladus glanduliferus var. australis (G)	Cal. desert; Ariz.
Eriophyllum lanosum	Cal. desert; Ariz.
Ambrosia pumila	Cal. coast
Coreocarpus parthenioides	BC
Dyssodia anthemidifolia (S)	BC
Gnaphalium oxyphyllum (S)	BC
Gnaphalium palustre	Cal. coast
Malacothrix californica var. glabrata (G)	Cal. desert; Ariz.
Malacothrix Xanti (S)	BC
Malperia tenuis	BC
Nicolletia trifida	BC
Palafoxia linearis	Cal. desert; Ariz.
Parthenice mollis	Ariz.; Son.
Pectis ambigua	BC
Pectis papposa	Cal. desert; Ariz.
Perityle aurea	BC
Perityle Emoryi	Cal. coast and desert; Ariz.
Perityle lobata	BC
Perityle californica	Son.
Senecio mohavensis	Cal. desert; Ariz.
Stylocline micropoides	Cal. desert; Ariz.

The above table serves to suggest the geographic relationships of the ephemerals of Baja California, although it is based only on a fraction of the total number. As listed, the abundant species are about equally divided between endemics and species also occurring in the Sonoran Desert in California and Arizona, chiefly in the Lower Colorado Valley. A large percentage of the latter group extend into the Arizona Upland and northwestern Sonora, but do not range south of Tiburón Island. Most of the endemic ephemerals of Baja California are found in

the southern half of the peninsula. Only two species are listed which occur on both sides of the Gulf without being known in California or Arizona.

The distributional features indicate a strong similarity in the winter ephemeral flora throughout the Lower Colorado Valley, the Central Gulf Coast, and the Vizcaíno Region. The Magdalena Region is not so closely related to the areas in the north. The ephemerals are distinctly an element of the desert flora. The ephemerals of coastal California and of the desert-chaparral transition in Baja California have many generic relationships to the desert ephemerals, but the cases of specific identity in the two groups are probably not more than 15 per cent of the number of coastal forms.

Winter Ephemerals of California and Arizona

As an element of the vegetation, the winter ephemerals retain their importance in the Sonoran Desert to its northern and northeastern limit, but the number of species decreases slightly toward the north and considerably toward the east. In favorable seasons they are most conspicuous on the sandy plains of the Lower Colorado Valley, where they often form an open carpet of green, followed by unrivaled displays of flowers. On the active dunes there are few ephemerals, and on the stony plains they are usually widely spaced. Many of the winter ephemerals range only to the limits of the desert or a very short distance beyond it. In the neighboring regions the spring display of verdure and flowers is almost wholly derived from herbaceous perennials.

South of the valley of Río Magdalena and the Plains of Sonora the winter ephemerals become a minor feature of the vegetation. A few species, notably *Perityle californica*, may be locally abundant, but the display is not general and the number of species involved is small.

The most abundant winter ephemerals of the sandy areas around the head of the Gulf of California are the following:

Festuca octoflora
Eriogonum reniforme
Eriogonum Thomasii
Eriogonum trichopes
Chorizanthe rigida
Chorizanthe brevicornu
Chorizanthe Thurberi
Nemacaulis denudata
Abronia villosa
Calyptridium monandrum
Achyronychia Cooperi
Eschscholtzia minutiflora
Dithyraea californica
Hosackia tomentella
Lupinus sparsiflorus var. arizonicus
Lupinus concinnus
Euphorbia melanadenia
Stillingia spinulosa
Stillingia linearifolia
Eremalche rotundifolia
Eremalche exilis
Petalonyx Thurberi
Oenothera decorticans var. condensata
Oenothera brevipes
Oenothera clavaeformis vars.
Nama demissum
Gilia floccosa
Langloisia setosissima
Cryptantha angustifolia
Eremocarya micrantha
Pectocarya linearis var. ferocula
Salvia columbariae
Plantago insularis var. fastigiata
Nemacladus ramosissimus

Monoptilon bellioides
Stylocline gnaphalioides
Dicoria canescens
Geraea canescens
Palafoxia linearis
Eriophyllum Wallacei
Chaenactis stevioides
Gaillardia arizonica
Psathyrotes annua

In the Arizona Upland the abundance of winter ephemerals is, as elsewhere, determined by the amount and frequency of the late winter rains. In very dry seasons the display of ephemerals is limited to small plants of *Plantago insularis* var. *fastigiata*, *Lesquerella Gordoni*, and the introduced *Sisymbrium irio*. In favorable seasons the ephemerals make an almost continuous ground cover on level areas with fine retentive soil, grow abundantly in the light shade of shrubs, and form very open stands on slopes or plains with a gravelly surface. The period of their best development usually extends from early in March to the middle of April. The predominant flower colors are white and yellow. Nowhere in this region are there such patches of vivid color as are made by *Abronia villosa* in the Lower Colorado Valley or by the various species of *Gilia* in the Mojave Desert.

The following list includes the characteristic winter ephemerals of the Arizona Upland. So much interest attaches to the distributional ranges of these plants that the table has been drawn up to indicate those found in the Mojave Desert (MD), those extending south into the inner part of the desert in Sonora (Son.), those occurring in the Great Basin (Utah, Nev.), and those extending east into western Texas (Tex.).

Bromus arizonicus	Cal. (coast)			
Festuca octoflora	MD			Tex.
Muhlenbergia microsperma	MD	Son.		
Poa Bigelovii	MD		Nev.	Tex.
Parietaria floridana	MD	Son.		
Pterostegia drymarioides	MD		Utah	
Chorizanthe brevicornu	MD	Son.	Nev.	
Chorizanthe rigida	MD	Son.		
Eriogonum deflexum	MD		Utah	
Eriogonum trichopes	MD		Utah	
Eriogonum inflatum	MD			
Eriogonum Abertianum				Tex.
Eriogonum polycladon				Tex.
Eriogonum angulosum	MD		Utah	
Monolepis Nuttalliana	MD	Son.	Utah	Tex.
Calandrinia ciliata	Cal. (var. on coast)			
Calyptridium monandrum	MD			
Loeflingia texana		Son.		Tex.
Myosurus cupulatus	Cal.	Son.		
Platystemon californicus	MD			
Eschscholtzia mexicana			Utah	Tex.
Streptanthus arizonicus		Son.		
Lepidium lasiocarpum	MD	Son.	Utah	Tex.

Dryopetalon runcinatum		Son.		Tex.
Lesquerella Gordoni	MD	Son.		Tex.
Lesquerella purpurea				Tex.
Draba cuneifolia var. integrifolia	MD	Son.	Utah	Tex.
Descurania pinnata subspp	MD	Son.	Nev.	Tex.
Thysanocarpus amplectens			Utah	
Oligomeris linifolia	MD	Son.		Tex.
Tillaea erecta	Cal. (coast)			
Lupinus sparsiflorus var. arizonicus	MD	Son.	Nev.	
Lupinus concinnus	MD		Utah	
Hosackia brachycarpa	MD			
Hosackia humilis	MD			
Astragalus austrinus	MD	Son.	Utah (var.)	Tex.
Erodium texanum	MD			Tex.
Euphorbia eriantha		Son.		
Sphaeralcea Coulteri		Son.		
Eremalche exilis	MD			
Mentzelia albicaulis	MD		Nev.	
Mentzelia aspera				
Mentzelia nitens	MD		Utah	
Oenothera leptocarpa	MD			
Oenothera clavaeformis vars	MD			
Oenothera chamaenerioides	MD	Son.		Tex.
Oenothera primiveris	MD	Son.		Tex.
Gaura parviflora var. lachnocarpa		Son.		
Spermolepis echinata		Son.		Tex.
Daucus pusillus	MD	Son.		Tex.
Bowlesia incana	MD			Tex.
Linanthus aureus	MD			Tex.
Linanthus Bigelovii	MD		Utah	Tex.
Gilia filifolia var. diffusa	MD			Tex.
Gilia stellata	MD	Son.	Nev.	Tex.
Gilia sinuata			Nev.	
Pholistoma auritum var. arizonicum	Cal. (coast, the sp.)			
Eucrypta chrysanthemifolia var. bipinnatifida	MD			
Eucrypta micrantha	MD	Son.		Tex.
Phacelia distans	MD			
Phacelia Popei var. arizonica		Son.		Tex.
Phacelia crenulata	MD		Utah	Tex.
Nama demissum	MD		Utah	
Nama hispidum vars	MD (var.)			Tex.
Harpagonella Palmeri var. arizonica	Cal. (coast, the sp.), Son.			
Pectocarya heterocarpa		Son.	Utah	
Pectocarya linearis var. ferocula	Cal. (coast, var.)			
Lappula texana var. coronata				Tex. (the sp.)
Lappula Redowskii var. desertorum	MD (the sp.)			Tex. (the sp.)

Eremocarya micrantha	MD		Nev.	Tex.
Cryptantha angustifolia	MD		Utah	Tex.
Cryptantha pterocarya	MD		Nev.	Tex.
Cryptantha barbigera	MD		Utah	
Plagiobothrys arizonicus	MD		Nev.	
Plagiobothrys Pringlei				
Amsinckia intermedia	MD			
Amsinckia tessellata	MD		Utah	
Salvia columbariae	MD			
Petunia parviflora	Cal. (coast)		Son.	Tex.
Orthocarpus purpurascens	MD			
Plantago Purshii	MD			Tex.
Plantago insularis var. fastigiata	MD		Nev.	
Galium proliferum	MD		Utah	Tex.
Nemacladus glanduliferus var. orientalis				
Greenella arizonica		Son.		
Monoptilon bellioides	MD	Son.	Utah	
Stylocline gnaphalioides	MD			Tex.
Evax multicaulis	MD			Tex.
Filago californica	Cal. (coast)			
Filago arizonica	MD			
Layia glandulosa	MD		Nev.	
Baeria chrysostoma var. gracilis	MD			
Eriophyllum lanosum	MD		Utah	
Perityle californica		Son.		
Chaenactis carphoclinia	MD		Nev.	
Chaenactis stevioides	MD		Nev.	
Gaillardia arizonica				
Dyssodia concinna		Son.		
Pectis Palmeri		Son.		
Pectis prostrata		Son.		
Microseris linearifolia	MD			
Stephanomeria exigua			Nev.	Tex.
Rafinesquia neomexicana	MD		Utah	Tex.
Malacothrix Coulteri	MD		Utah	
Malacothrix californica var. glabrata	MD		Utah	
Malacothrix sonchoides	MD	Son.	Nev.	
Calycoseris Wrightii	MD	Son.	Utah	Tex.
Senecio monoensis	MD	Son.	Utah	

The winter ephemerals just listed show their strongest geographical affinity with those of the Mojave Desert. Out of the total of 109 species in the Arizona Upland, 73 are represented in the Mojave Desert by plants which are specifically identical or of varietal relationship. As there are 496 species and varieties of winter ephemerals in the Mojave Desert, it appears that only one-seventh of them extend eastward into the Arizona Upland, although they form there the dominant element in that group of plants. The Californian element is further strengthened

by the occurrence of 8 species in Arizona which are found on the coast but not in the Mojave Desert. Many plants of the Mojave and Sonoran Deserts are found in the Great Basin Desert only in extreme southern Nevada and Utah. Among the 43 ephemerals common to the Great Basin and the Sonoran Desert are a number which are confined to the south, but also several which range north into Oregon and Washington.

There are not more than 12 or 15 winter ephemerals in Arizona which are absent from the Mojave Desert and either are endemic to Arizona or extend east to Texas. There are 42 species which range into western Texas, of which 31 occur in the Mojave Desert or on the California coast. Because of the later arrival of spring, the season of activity for the ephemerals in Texas ranges from the middle of April to the end of May.

Any speculation as to the geographical source of the winter ephemerals must not overlook the fact that the relatively large number of species common to west Texas and the Sonoran Desert is so largely made up of forms extending east from the Mojave Desert.

The number of winter ephemerals in the upland parts of northern Sonora is much smaller than that on the sandy plains of northwestern Sonora. The 38 species that have been recorded are possibly not all the forms that might be found there. Three of them, *Perityle californica*, *Dyssodia concinna*, and *Astragalus austrinus*, are not found in the United States. One of them, *Pectis prostrata*, is a summer ephemeral in Arizona. Several other summer ephemerals of the northern part of the Sonoran Desert have been observed in small colonies south of Guaymas in the late winter, including *Kallstroemia grandiflora*, *Tidestromia lanuginosa*, and *Pectis papposa*.

Summer Ephemerals

The herbaceous plants which appear after the first heavy rains of summer are as abundant and ubiquitous as the winter ephemerals. After successive copious rains they carpet the plains and gentle slopes, in places where the surface had previously been bare for three or four months. The seedlings begin to appear about three days after the first heavy rain, and their growth is even more rapid than in the case of the winter ephemerals. In the Arizona Upland there are very few years in which conditions are favorable for their start earlier than July 10. Rarely there are heavy showers in May, followed by a short period of moist soil. A few colonies of summer ephemerals have been observed after these pre-seasonal rains, but in no case have the plants persisted until the usual time of the summer rains.

In general, the season for summer ephemerals is longer than that for winter ephemerals, and the moisture of the soil is higher and more continuously maintained. A few summer ephemerals are of low habit, but the majority reach a height of 3 to 4 dm., and a few commonly grow to 2 m. Many of them are more abundant on disturbed ground than in wholly natural situations, and have many of the characteristics of weeds. Grasses are much more richly represented in the

summer than in the winter, both in species and in individuals. The number of species of summer ephemerals is smaller than the number of winter species, but their role in the vegetation is just as important.

The foliage of the summer ephemerals is prevailingly mesic, and in only a few cases provided with wool, hair, air-containing epidermis, or heavy cutinization. In a few species the leaves are more than 25 sq. cm. in area (*Helianthus petiolaris*, *Xanthium spinosum*), and in a larger number they are more than 10 sq. cm. (*Datura meteloides*, *Parthenice mollis*, *Amaranthus Palmeri*). Simple leaves are more common than compound, and very small leaves or leaflets are found only in the several species of *Euphorbia* and in a few Compositae.

Geographic Distribution of Summer Ephemerals

In southern California and in Baja California the Sonoran Desert is extremely poor in summer ephemerals. After the summer rains which very infrequently visit the interior of southern California, a few of the commonest herbs of the region farther east may be found. In the Imperial Valley and on the plains west of Blythe, California, the following species have been noted over a period of 10 years:

Pectis papposa
Bouteloua aristidoides
Kallstroemia grandiflora
Amaranthus Palmeri
Boerhaavia coccinea
Euphorbia micromera
Euphorbia pediculifera
Datura discolor

In Baja California summer rains occur exceptionally on the Gulf coast at long intervals, and probably a few of the summer ephemerals are active at such times. No definite observations have been made other than the finding of dead remains of a few recognizable plants, as noted previously.

The following list includes all the widely distributed and frequently noted native summer ephemerals in the Arizona Upland and the Plains of Sonora, and probably comprises 75 per cent of the total number of plants of this group in the Sonoran Desert. Those indicated by the abbreviation (Tex.) range eastward to Texas.

Eragrostis arida (Tex.)
Sporobolus patens
Aegopogon cenchroides
Leptochloa panicea (Tex.)
Leptochloa viscida (Tex.)
Chloris virgata (Tex.)
Bouteloua aristidoides (Tex.)
Bouteloua barbata (Tex.)
Digitaria sanguinalis (Tex.)
Eriochloa gracilis (Tex.)
Panicum arizonicum (Tex.)
Panicum hirticaule (Tex.)
Panicum pampinosum
Setaria Grisebachii (Tex.)
Cenchrus echinatus (Tex.)
Cenchrus pauciflorus (Tex.)
Cenchrus Palmeri
Hackelochloa granularis
Cyperus aristatus var. inflexus
Atriplex elegans (Tex.)
Amaranthus Palmeri (Tex.)
Amaranthus fimbriatus (Tex.)
Amaranthus blitoides (Tex.)
Amaranthus graecizanus (Tex.)

Tidestromia lanuginosa (Tex.)
Allionia incarnata (Tex.)
Boerhaavia erecta (Tex.)
Boerhaavia gracillima (Tex.)
Boerhaavia coccinea (Tex.)
Boerhaavia megaptera
Boerhaavia spicata
Boerhaavia Coulteri
Boerhaavia intermedia (Tex.)
Boerhaavia pterocarpa
Boerhaavia purpurascens (Tex.)
Mollugo verticillata (Tex.)
Mollugo cerviana (Tex.)
Trianthema portulacastrum (Tex.)
Portulaca parvula (Tex.)
Cleome tenuis
Sphinctospermum constrictum
Desmodium procumbens
Crotalaria pumila
Kallstroemia grandiflora (Tex.)
Kallstroemia californica
Euphorbia serpyllifolia (Tex.)
Euphorbia micromera (Tex.)
Euphorbia pediculifera
Euphorbia setiloba
Euphorbia gracillima
Euphorbia florida
Euphorbia polycarpa
Anoda cristata (Tex.)
Quamoclit coccinea (Tex.)
Ipomoea hirsutula (Tex.)
Heliotropium curassavicum (Tex.)
Chamaesaracha coronopus (Tex.)
Quincula lobata (Tex.)
Conobea intermedia
Datura meteloides (Tex.)
Datura discolor
Martynia parviflora (Tex.)
Martynia arenaria (Tex.)
Houstonia prostrata
Diodia teres var. angustata
Mitracarpus hirtus (Tex.)
Haplopappus gracilis (Tex.)
Haplopappus spinulosus subspp. (Tex.)
Psilactis Coulteri (Tex.)
Aster exilis (Tex.)
Parthenice mollis
Iva ambrosiaefolia (Tex.)
Ambrosia aptera (Tex.)
Ambrosia psilostachya (Tex.)
Xanthium spinosum (Tex.)
Xanthium pennsylvanicum (Tex.)
Eclipta alba (Tex.)
Helianthus petiolaris (Tex.)
Psilostrophe Cooperi
Baileya multiradiata (Tex.)
Hymenothrix Wislizeni
Bahia absinthifolia var. dealbata (Tex.)
Pectis linifolia
Pectis papposa (Tex.)

As already noted, the summer ephemerals are poorly represented in both species and individuals west of the Colorado River and the Gulf of California. Nearly all the species listed have been observed or collected in northern Sonora, and several species have been found in Sonora which do not occur in the United States.

The distributional features of the winter and summer ephemerals are exactly opposed. The former are very richly represented in the California deserts and diminish toward the east, whereas the latter are largely found also in the desert areas of western Texas and diminish rapidly in western Arizona. These features are closely correlated with the seasonal distribution of rainfall. It seems highly probable that these two groups of herbaceous plants have retained their distinctive characteristics and their general distributional pattern for a long period of geological time.

5

Ecological Features of Characteristic Species

A COROLLARY to the simplicity of desert vegetation is the extreme abundance of many of its species. Over large areas the same type of situation is characterized by abundant stands of the same small number of species. The uncommon plants occasionally found are usually near the limits of their distributional range, in some part of which they also are very abundant. Nearly every one of the perennials of the Sonoran Desert which is ordinarily infrequent has been found in great abundance in one or more restricted localities, often being the dominant plant. In the desert there is little suggestion of the localized occurrence and limited range which add so much to the diversity of the flora in moist warm regions.

The vegetative dissimilarity of many of the abundant desert plants is accompanied by differences in ecological behavior and physiological response which make almost every species a distinct entity requiring separate investigation. General statements can be made only for the members of a few well represented life forms, such as the deciduous compound-leaved shrubs or the platyopuntias.

The purpose of this chapter is to describe the distribution, habitats, and ecological characteristics of a few of the commonest plants of the Sonoran Desert. The individuality of the desert plant seems to make this a necessary supplement to the description of the vegetation. The uneven treatment of the various species is due to their particular features, as well as to the fact that some have been more accessible for study than others.

The maps showing distribution are based chiefly on notes made by the author in field work in this region. Only a few of the localities are substantiated by herbarium specimens. The clear identity of the species involved made it unnecessary to multiply the number of collections. A few localities have been added on the basis of published records (mostly those of Brandegee and of Goldman in Baja California) or of collections in the herbaria of Stanford University, the University of California, and the University of Arizona.

After the treatments of some of the species are given citations to papers which bear on their ecological features. The copious literature on *Carnegiea* has been listed only in part, since the titles cited contain references to most of the other papers. On many of the plants no specific work has been done, and there is nothing in botanical literature about them except brief taxonomic descriptions.

Acacia constricta (Mimosaceae)

This shrub is abundant throughout the northern part of the Sonoran Desert and sparingly represented farther south. It is abundant along streamways, but grows in all

situations in the Arizona Upland. Pure stands are rare, as it is commonly associated with *Larrea* and other shrubs. It is commonly from 2 to 3 m. in height and rarely exceeds 4 m. in the most favorable situations. The bark of the larger stems is rough and gray; that of the twigs and smaller stems is smooth and reddish brown. The form of the crown is extremely variable, and the manner of branching has no unusual features. The young stems are armed with straight white spines from 2 to 5 cm. in length. *Acacia constricta* is deciduous, but is unlike other winter-deciduous shrubs in renewing its foliage in the spring only in case it has an adequate water supply. This means that in a dry spring the favorably situated individuals will come into leaf early in April, whereas the plants growing away from streamways will remain leafless 8 or 10 weeks longer, coming into leaf only after the beginning of the summer rains. The leaves are decompound, the branches bearing from 5 to 8 pairs of leaflets from 1 to 2 mm. in length. Nyctitropic and drought movements are executed by the leaflets. The foliage may begin to fall at any time from late September to late November, according to the autumn rainfall. The flowers of *A. constricta* form small yellow balls borne on pedicels several times longer than their diameter. The fruit is a pod from 5 to 10 cm. long, constricted between the seeds. With ample rainfall the crop of seeds is large and the opening of the pods is immediate. Rodents take their usual heavy toll of the crop, but many seeds fall on the sand of small arroyos and are widely disseminated by succeeding rains. Germination is delayed for at least 12 months by a coating of wax.

Acacia cymbispina (Mimosaceae) ESPINO

This is the dominant tree of the coastal plain of Sinaloa, and is abundant in the southernmost part of the Sonoran Desert. Its northern limit is a few kilometers northeast of Hermosillo and in the region near the confluence of Río Sonora and Río San Miguel, where it is confined to the margins of streamways but reaches its customary size and features of development.

Acacia cymbispina is a widely branched, slender, symmetrical tree, usually with a single trunk and wide-spreading branches. The top of the crown is flat, and the canopy of foliage is so thin and open that only a very light shade is thrown by the largest trees. The stout boat-shaped spines are 2 to 4 cm. in length and dark in color when young, and give the tree a distinctive appearance. The growth of young trees is very rapid and soon closes roads and trails which pass through the heavy stands.

Acacia Greggii (Mimosaceae) CATCLAW. UÑA DE GATO

Although most commonly seen as a shrub from 1 to 2 m. in height, *Acacia Greggii* is sometimes found as a low-branching tree 5 to 8 m. in height with a trunk 20 to 40 cm. in diameter. It is easily distinguished from *A. constricta* by the more open and spreading habit, by the larger leaflets, and by the gray bark throughout the plant. In all individuals there are many long, unbranched shoots extending out from the crown and armed with short, curved spines. The decompound leaves bear from 3 to 5 pairs of leaflets from 3 to 6 mm. long. Like the other mimosaceous plants, *A. Greggii* shows nyctitropic and drought movements of the leaves. The flowers are borne in long racemes and are pale buff. The pods are 10 to 15 mm. wide and are usually curved in several planes. The seeds are broader and flatter than those of the other acacias, but undergo a similar delay in germination due to a waxy coating.

Acacia Greggii is widely distributed throughout the Sonoran Desert, but is most abundant in its eastern half. It is particularly abundant on upper bajadas in the Arizona Upland and along the streamways of that area. It extends far beyond the limits of the Sonoran Desert and often appears as an isolated individual of maximum size. The foliage persists through all but the most severe winters, falling gradually during the growth of new leaves in April or May. A severe frost will kill the leaves, but they will remain on the plant for several weeks or until the advent of spring growth.

Acacia Willardiana (Mimosaceae) PALO BLANCO

A slender tree of 6 to 8 m., conspicuous by reason of its white exfoliating bark and long, slender cladophylls (pl. 33). It is found only on rocky slopes and is particularly abundant on crests and ridges which afford little soil. It is rare north of the Río Sonora, but becomes a characteristic plant of the hills in the southern part of the Plains of Sonora. Slopes covered with a very open but evenly spaced stand of trees of uniform height give the first forecast of the extensive acacia thorn forest which lies south of the Sonoran Desert. *Acacia Willardiana* is the only woody plant in the Sonoran Desert with well developed cladophylls. The leaves are reduced to one or three short-lived pinnae, which appear on the seedling and on the first shoots of the seasonal growth. Nearly all the photosynthetic performance of the tree is carried on by the cladophylls.

Bursera microphylla (Burseraceae) COPAL

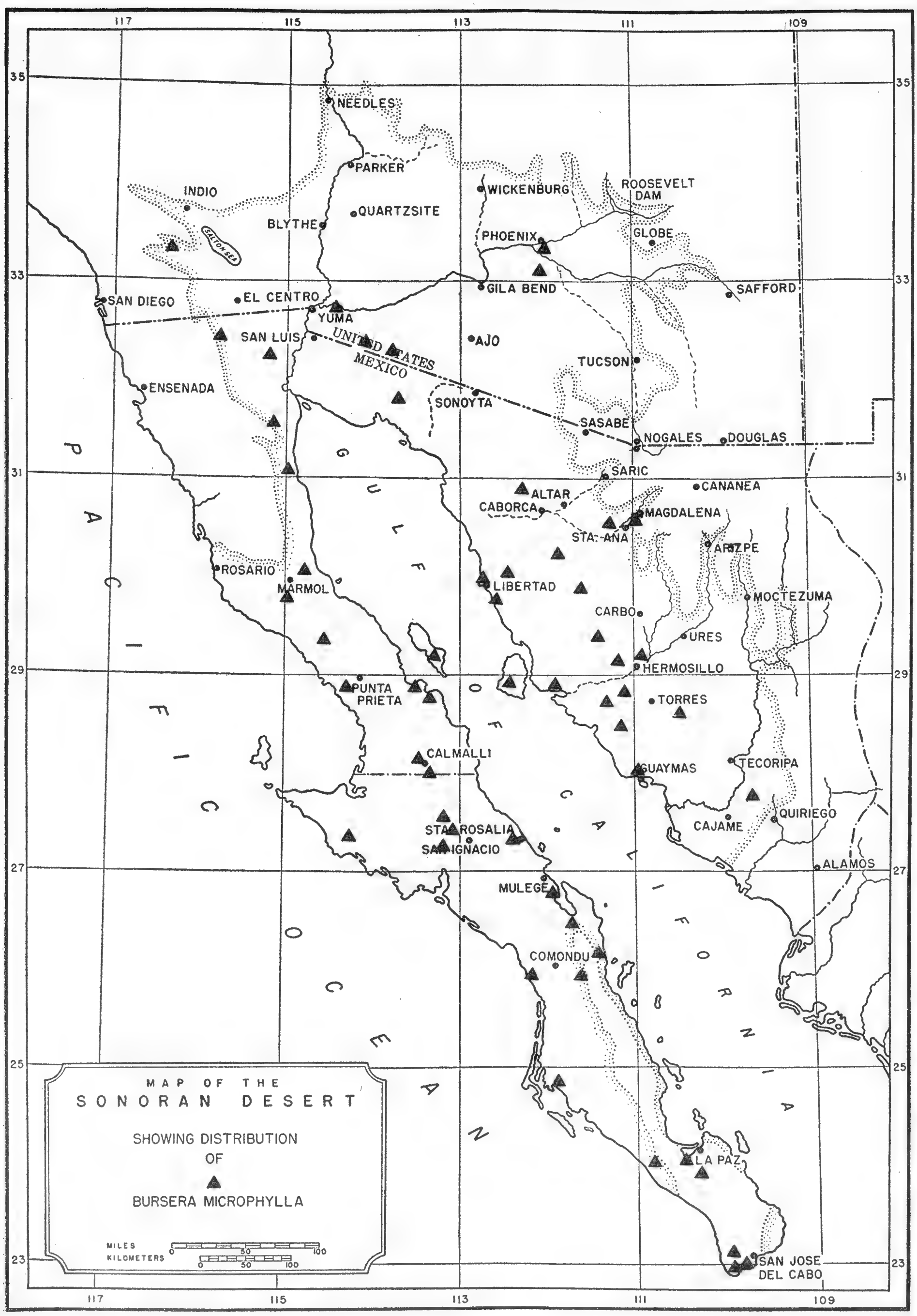
(Map 4)

In its best development this is one of the handsomest and most striking trees of the Sonoran Desert. It is low-branching but reaches a maximum height of 10 to 12 m. The trunk and lower limbs are thickened out of proportion to the height of the tree, but there is no thickening of the endmost branches and twigs. The tree is commonly richly branched, with a smooth gray or bronze-red surface and no tendency to form secondary bark. The leaves are simply pinnate and dark green. The foliage is evergreen but liable to killing in severe winters. If not so killed, the leaves persist from one growing season to the next, and many of them appear to persist for two or even three years.

The thickness of the trunk is due to extensive development of the cortex, which accounts for 60 to 70 per cent of the basal diameter. The wood is soft, and the tissue of the cortex is very soft and impregnated with gum, resin, and latex, which flow copiously from a freshly cut trunk. In the seedling the first indications of the thickening are given by the development of a small, almost spherical enlargement just at the surface of the ground. The excessive development of cortex proceeds gradually up and down from this enlargement.

The seeds of *Bursera microphylla* have a shiny black coat and germinate readily. The number of well established seedlings to be found is greater than in the case of other xeric trees, but there is severe mortality among the young plants from 10 to 40 cm. in height.

The distribution of *Bursera* is almost coincident with the extent of the Sonoran Desert. The tree is absent only from the most northern and eastern parts of the desert, and extends beyond it only in the Cape Region of Baja California. It is uncommon north of Rosario and the Río Magdalena, and shows its best development as to size and numbers in central Baja California and central Sonora. No pure stands have been seen, and there are rarely more than 8 or 10 trees to a hectare.



Map 4. Distribution of *Bursera microphylla*

Carnegiea gigantea (Cactaceae) SAHUARO

(Map 5)

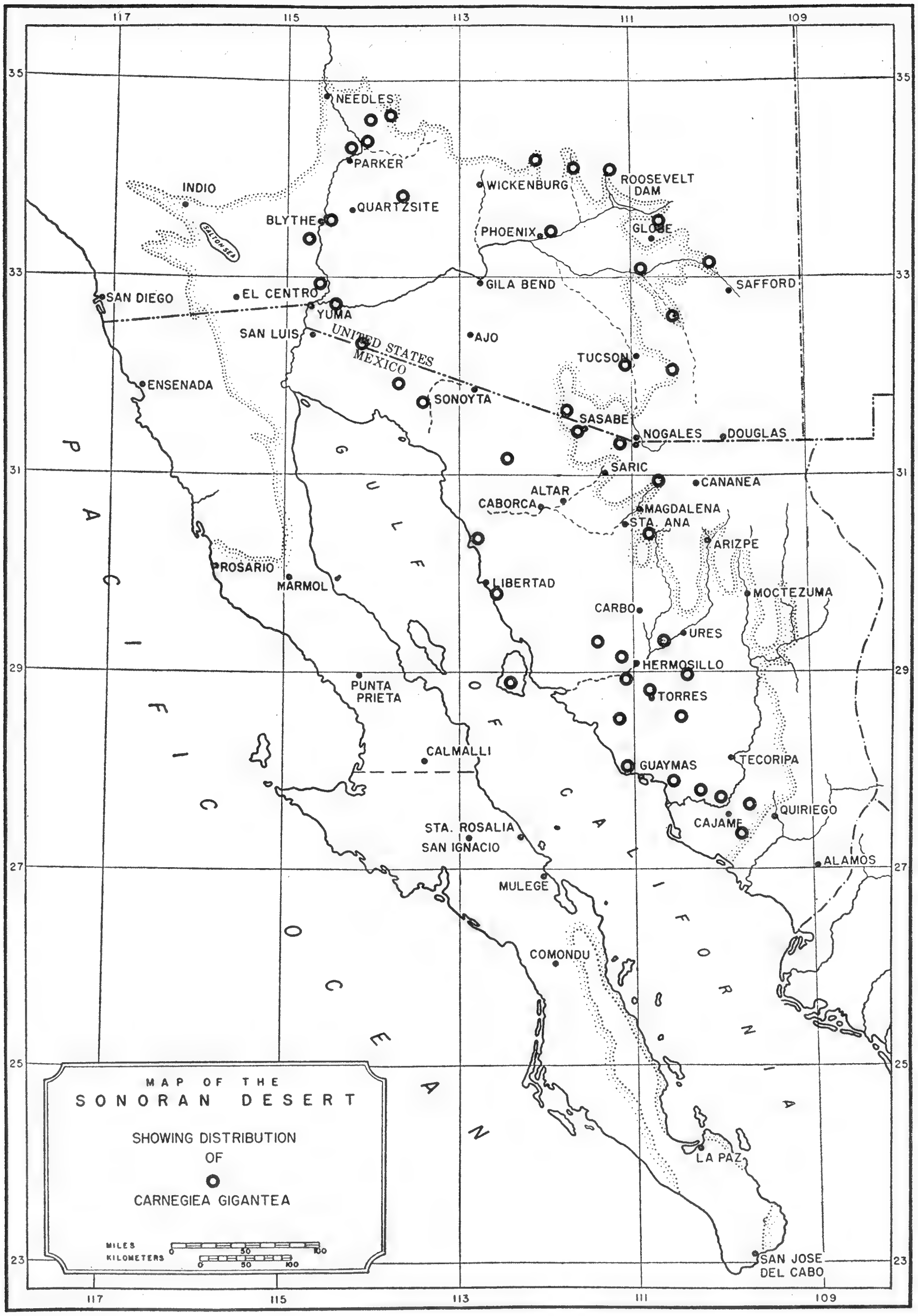
Carnegiea is the best known of the characteristic plants of the Sonoran Desert. Its size and graceful form make it conspicuous in any locality, and its position as the northernmost of the many massive columnar members of the cactus family has made it the subject of numerous ecological, anatomical, and morphological investigations.

The height of *Carnegiea* at maturity is 10 to 12 m., or slightly more in exceptional cases. The young plant is a grooved cylindrical column, rising from a slender base 15 to 20 cm. in diameter, and reaching a thickness of 30 to 40 cm. at a level well above the middle of the plant. Branches usually appear on plants 5 to 8 m. high, and there are frequently 5 or 6 primary branches, although the number may be much greater in the oldest individuals. Secondary branches are found only on large plants and are never numerous. The water content is from 75 to 95 per cent of the green weight, being greater at the top and less at the base. Old trees with numerous branches have been calculated to weigh as much as 6 or 7 tons.

The root system of *Carnegiea* is little more than 1 m. in depth, but extends laterally near the surface for as much as 30 m. A stout but elastic woody skeleton extends from base to top, and consists of a cylindrical group of rods, anastomosing to middle height and free above. The remainder of the plant is a soft parenchyma of high water content and richly impregnated near the base with crystals of calcium silicate. The chlorophyll-bearing tissue blankets the plant from the top to the rough gray bark which clothes the slender base. Clusters of very stout spines are borne on the ridges of younger plants, but slender, limber ones take their place at higher levels on old trees.

The flowers of the sahuaro are borne near the apex of the trunk and larger branches, or exceptionally at widely separated intervals for a distance of 1 m. or more from the tip. The flowers open during the second or third week of May and are chiefly pollinated by bees. The fruits develop rapidly and are mature by the middle of June. The number of fruits on a large plant may be as great as 200, and there are approximately 1000 seeds in each fruit. The seeds are nearly spherical and about 1.5 mm. in diameter. The abundant seed crop stands in strong contrast to the very small number of new individuals that become established even in the most favorable years. The seeds are borne in a sweet, juicy pulp which is eagerly eaten by birds. In the case of seed-eating birds, this means the destruction of all the seeds eaten. In the case of other birds, the seeds are passed without loss of viability. A heavy toll of the seed crop is taken by ants, which remove the small embryo and store the seeds. Rodents and coyotes eat the seed-bearing pulp and destroy a small percentage of the seeds eaten. The fact that the seed crop matures from 2 to 4 weeks before the first summer rains bring favorable conditions for their germination gives a full opportunity for the various predators to decimate the crop. The seedling is very small and provided with a short, poorly branched root, which results in many seedlings' being covered or washed out during the rains immediately following germination. It is doubtful whether more than half a dozen seedlings persist to the following year from a crop of many thousands of seeds.

The early growth of the seedlings of *Carnegiea* is very slow. After 2 or 3 years they are only a few mm. in height, and after 10 years they are not more than 1.5 to 2 cm. in height. The later growth is so variable that the age of a plant 1 m. high may be from 20 to 50 years. After a height of 2 to 3 m. is reached, the growth rate is about 10 cm. per year in the main trunk and slightly less in the large branches. The age of the



Map 5. Distribution of *Carnegiea gigantea*

largest individuals has been estimated from the known growth rate to be from 150 to 200 years. Wounds and infections are quickly walled off by the formation of callus. Nests made in the sahuaro by woodpeckers are lined with a heavy bag-shaped callus, often to be found in sound condition in the rotting remains of fallen trees. The principal natural cause of injury is the breaking of branches by high winds. The broken surface heals quickly in dry weather, but in a rainy period it usually leads to infection and the rapid death of the entire plant. The principal cause of death is overturning by wind or by the removal of soil and stones from the base of the tree, or because of the softening of the soil by prolonged rain.

The range of *Carnegiea* coincides closely with the boundary of the Sonoran Desert from the Colorado River east and south to the valley of the Río Sonora. Its altitudinal limit in this stretch is about 1200 m., but occasional individuals are found as high as 1500 m. on steep south slopes. In southern California the sahuaro is found in only three localities close to the Colorado River, and in Baja California it has never been observed. In northwestern Sonora it is absent from the sandy plains adjacent to the Gulf, but is abundant on most of the low mountains. Heavy stands are increasingly rare south of Tiburón Island, and it has not been reported near the coast in the area between San Carlos Bay and the mouth of the Río Yaqui. In the interior south of the Río Sonora the stands of sahuaro are infrequent and open. The southernmost individuals that have been noted are on hills about 15 km. south of Cajeme (Ciudad Obregón), Sonora. It has been reported as occurring in the lower valley of the Río Fuerte in northern Sinaloa, but the observation is open to doubt.

The finest stands of sahuaro are on the coarse outwash slopes of mountains in southern Arizona, south of the Gila River and east of Ajo, Arizona. The size and abundance of the plants are greatest on slopes of southern or southwestern aspect, and on the lower slopes of the adjacent hills. In no part of its range is the sahuaro found on flood plains or alluvial flats. Its best habitats are localities in which there is rock in place or a soil well filled with large angular rocks, in either of which situations a firm anchorage is supplied for the root system. A single large colony has been seen on coarse alluvial level soil between Chandler, Arizona, and the Gila River; here the cactus was associated with *Atriplex polycarpa*. This colony has recently been completely destroyed by the clearing of the land for cultivation.

Literature

Johnson, Duncan S. The influence of insolation on the distribution and on the developmental sequence of the flowers of the giant cactus of Arizona. Ecology **5:** 70–82, 1924.

Shreve, Forrest. The rate of establishment of the giant cactus. Plant World **13:** 235–240, 1910.

——— The influence of low temperatures on the distribution of the giant cactus. Plant World **14:** 136–146, 1911.

Spalding, Effie S. Mechanical adjustment of the sahuaro (*Cereus giganteus*) to varying quantities of stored water. Bull. Torrey Bot. Club **32:** 57–68, 1905.

Ceiba acuminata (Bombacaceae) Pochote

The pochote, or kapok, is a small tree of 6 to 8 m., sparingly branched and with a very open crown. The trunk is stout at the base, tapers rapidly, and is covered with broad, blunt thorns which arise by secondary thickening from the slender thorns of the young tree. The leaves are palmate, with a spread of 15 cm. and an area of 65 to 100

sq. cm. They are distinctly mesic in structure and are present only in the summer rainy season. *Ceiba* is infrequent in the southern part of the Sonoran Desert, growing on level ground and low hills, but is conspicuous by reason of its light gray bark, tapering trunk, sparse and irregular branching, and large fruits.

Cercidium floridum (Caesalpiniaceae) BLUE PALO VERDE

There is a strong similarity between young plants of *Cercidium floridum* and those of *C. microphyllum*, but with increasing age a number of obvious differences develop. The former usually has a single trunk to a height of 1 to 2 m. with light gray bark, a rounded crown with many nearly horizontal branches, and stout end twigs bearing scattered thorns. The leaflets are about twice the diameter of those of *C. microphyllum*, and the foliage and branches are blue-green, in strong contrast with the yellow-green of the related tree. The flowers are deep yellow, in contrast with the pale yellow of *C. microphyllum*, and appear 2 or 3 weeks earlier.

The distribution of the two palo verde trees is much the same, but *C. floridum* extends beyond *C. microphyllum* in nearly all parts of their limit, particularly in the south on the coastal plain of Sinaloa. In the mountains *C. floridum* invariably reaches a slightly higher altitude. In the center of the distributional range there is a strong difference in the habitat preferences of the two, *C. microphyllum* being confined to the coarse soil of plains, outwash slopes, and hills, whereas *C. floridum* is most abundant on fine soil, on alluvial plains, and in or near the beds of streams. It is also sparingly found on sandy plains.

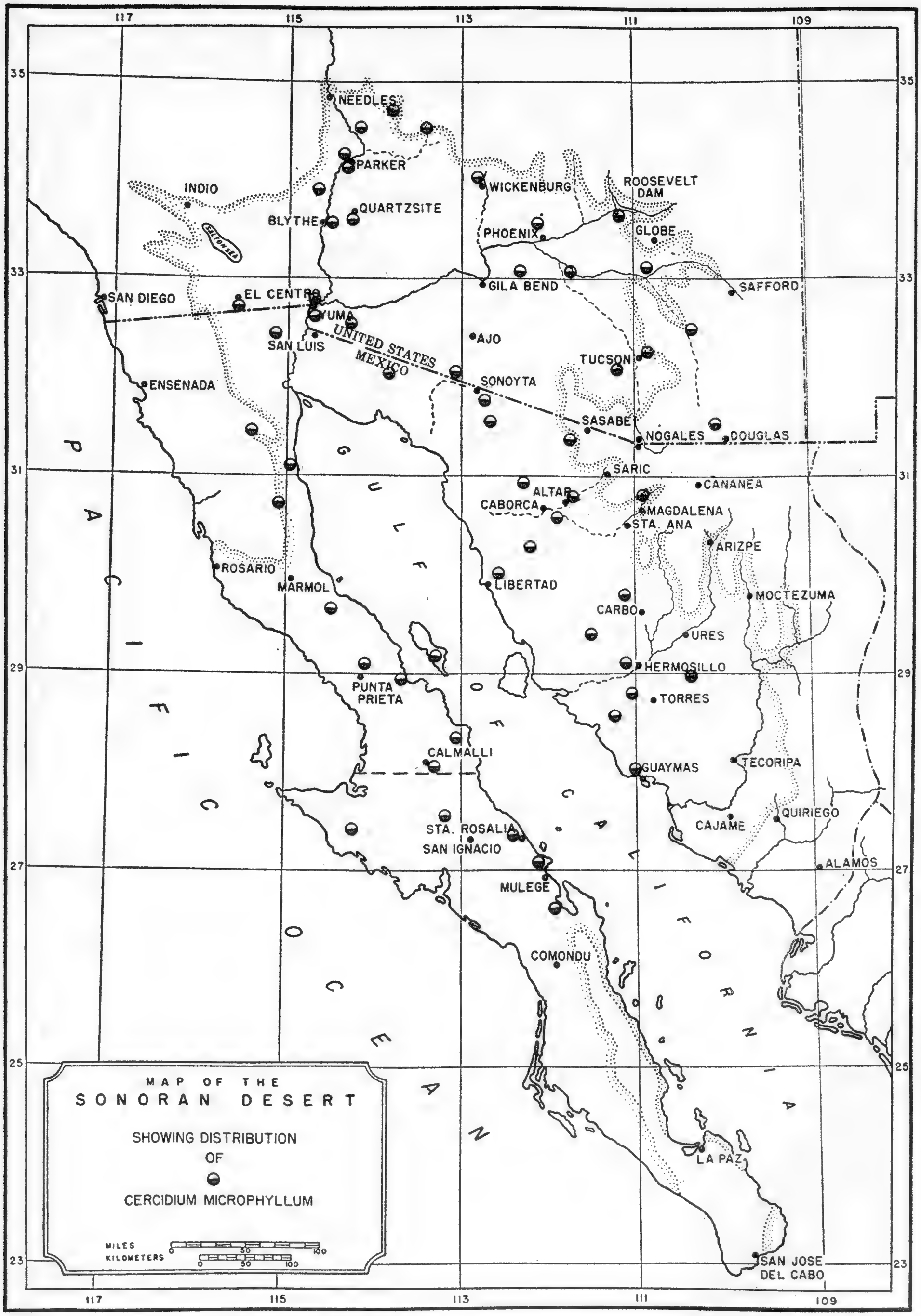
The oldest trees of *Cercidium* are 7 to 10 m. high and have a wide-spreading crown. The finest examples of it are found along the streamways of extreme southwestern Arizona and northwestern Sonora. It often occurs in continuous belts along the larger streamways, but large isolated trees are frequently found on small streamways. The seed and its behavior in germination are nearly the same as in *C. microphyllum*, but reproduction is better. In young trees less than 2 m. in height there are numerous horizontal or prostrate branches with very thorny twigs. Only on reaching an age of 30 to 50 years does the single trunk become dominant.

Cercidium microphyllum ((Caesalpiniaceae) PALO VERDE

(Map 6)

Among the green-stemmed microphyllous and aphyllous perennials of the Sonoran Desert, *Cercidium microphyllum* and *C. floridum* are by far the most abundant. With their almost constant difference of habitat, the common occurrence of these two small trees does much to give perennial greenness to the desert landscape. The presence or absence of the very small compound leaves makes only a slight change in the appearance of the trees except on close examination.

Throughout southern Arizona the distribution of *Cercidium microphyllum* conforms closely to the boundary of the desert, but isolated trees have been found beyond it on south slopes in a number of localities in southeastern Arizona. In southern California the tree is rare outside a few localities near the Colorado River. In Baja California *Cercidium* is nowhere so abundant as it is in Arizona, and it is absent from the Pacific side of the peninsula and the southern end south of Bahía Concepción. It is locally abundant between latitudes 27° and 30° N., but in this region rarely reaches the height



MAP 6. Distribution of *Cercidium microphyllum*

and spread attained on the Plains of Sonora. Except on the sandy plains of extreme northwestern Sonora, *Cercidium* is very abundant in that state as far south as Río Sonora. Toward the interior it becomes very infrequent in the long, narrow desert valleys which penetrate the desert grassland. Between Río Sonora and Río Yaqui *Cercidium microphyllum* is uncommon, and it has not been seen or reported south of the latter river.

Cercidium microphyllum commonly reaches a height of 5 to 6 m. and exceptionally 8 to 10 m. The trunk is greatly abbreviated and divides into two or three main branches at 10 to 25 cm. from the ground. The stems are richly branched, but the crown is not dense. The extreme base of the trunk is covered with a smooth, light gray bark which ends above at a very definite horizontal line. Observation of seedlings and young plants shows this line to be at the point of attachment of the cotyledons. Only rarely is this developmental vestige obliterated in the oldest trees. The smooth green surface of the rest of the tree is broken only by small patches of dark bark formed over wounds. The wood is light yellow, uniform in appearance and color from center to surface of the trunk, and very soft. Very close-set rings of seasonal growth are visible in carefully prepared sections.

The leaves of *Cercidium* are compound, with 3 to 5 pairs of nearly round leaflets 1 mm. or less in diameter. The leaves are borne in fascicles on older stems and in pairs on the growth of the season. There are commonly two crops of leaves, following the principal rainy seasons, and failing to appear if the rains do not take place. The leaves rarely persist more than 6 to 10 weeks. On the return of dry conditions the leaflets turn yellow and fall from the rachis, which in turn falls a few weeks later. On a tree in leaf the total area of the leaflets certainly does not exceed the total area of green stem surface, and is probably much less.

Flowers appear on *Cercidium* in April in central Sonora and about the middle of May in the Arizona Upland, provided there has been rainfall of the average amount or more. The trees either do not bloom at all or bloom very profusely, and there is little divergence in their behavior in different situations. The long, constricted pods ripen about 6 weeks after flowering, and without a definite mode of dehiscence soon liberate from 1 to 3 seeds. These are about 6 to 9 mm. in length, very slightly flattened, and with a heavy, dark brown, waxy coat. A large part of the seed crop is consumed by rodents, but the crop is so large that many seeds are left. Fresh seeds will not germinate until the coat has been scarified or the seeds washed in ether. Under natural conditions the wax coating is presumably removed by bacterial action, and the seeds are ready to germinate 12 months after they have been shed—or, in other words, at the first succeeding period of favorable moisture and temperature. The viability of the seeds is high, their germination takes place in about 3 days, and the number of seedlings appearing during the first week of the summer rainy period is very large. Seedlings reach a height of 2 to 3 cm. during July and August and develop a root system from two to three times the length of the shoot. During the dry weeks of autumn the mortality among the seedlings is very high, and it continues relatively high during their first 4 or 5 years.

The root system of *Cercidium* is deep and is also wide-spreading, but not superficially. The distribution of the roots is determined by the nature of the substratum on which a particular tree is growing. On rocky slopes the greatest penetration is through the pockets of soil and narrow fissures in the rocks, where small amounts of water penetrate and are prevented from further infiltration as well as from evaporation. For very young trees, successful establishment is primarily determined by the existence of a substratum which enables the roots to reach the lowest pockets of moist soil.

Exceptionally dry periods result in the death of twigs and branches, and sometimes of entire large limbs. Only very rarely does an entire mature tree die from drought. After a severe loss of branches, a large tree produces strong new shoots from the base. The oldest trees show evidence of having lost large limbs at intervals throughout their lives. The most careful estimate that is possible on large trees indicates that they reach an age of 300 to 400 years.

LITERATURE

SHREVE, EDITH B. The daily march of transpiration in a desert perennial. Carnegie Inst. Wash. Pub. 194, 1914.

SHREVE, FORREST. Establishment behavior of the palo verde. Plant World **14:** 289–296, 1911.

——— The establishment of desert perennials. Jour. Ecol. **5:** 210–216, 1917.

Cercidium sonorae (Caesalpiniaceae) BREA

This small tree resembles the other species of *Cercidium* in the complete greenness of its trunk and branches, but has a very different habit of growth (pl. 34). The trunk is erect and usually unbranched to a height of 1 to 2 m., and the branches are nearly horizontal, forming a flat, wide-spreading crown. All the surfaces have a matte deep green color and are covered with a minutely papillose coating of wax. The leaflets are slightly larger than in the other species of *Cercidium*, and the leaves are sparingly distributed throughout the crown. The flowers are borne in short fascicles widely distributed along the branches, in strong contrast with the terminal position of the inflorescences in the other species of *Cercidium*.

The northernmost individuals of the brea are to be found on the Plains of Sonora a few kilometers south of Santa Ana. It is never very abundant, and has not been observed in pure stands. Its greatest numbers and best development are south of Guaymas and in the southern tip of the Sonoran Desert. It has been seen at several localities in central Baja California, but is not abundant in any of them.

Cordia sonorae (Boraginaceae) PALO DE ASTA

Cordia is a small tree with a very open crown and large, rather mesic, simple leaves about 3 by 6 cm. in size. It is found only along streamways in the southern part of the Plains of Sonora, and is uncommon but very conspicuous on account of its large leaves. The trees are leafless during the dry spring months. Leaves appear during the summer rains and often persist through the winter, finally turning yellow and remaining in place for several weeks.

Encelia farinosa (Compositae) WHITE BRITTLEBUSH. INCIENSO

This small shrub has an open, hemispherical crown of foliage borne on sparsely branched stems. The trunk and principal branches are from 5 to 20 mm. thick. The plants rarely exceed 1 m. in height, and smaller plants are much more common. The leaves are light green, oval, petiolate, from 3 to 7 cm. in length. Leaves are borne during both the summer and the winter rains, and the two crops show differences in structure and physiological behavior. In the dry seasons the plant is without functioning leaves and is subject to the death of twigs and branches. Large drops of gum, very commonly used as incense, are exuded from the large stems and harden in place or fall to the ground.

They are particularly abundant in the driest habitats of the plant. The flowers are borne twice a year on long terminal peduncles, extending from 10 to 15 cm. beyond the foliage. Large crops of seeds are produced, from which a relatively large number of germinations take place. The number of young individuals to be found in a given season is closely dependent on the rainfall conditions of the preceding year or two.

Encelia occurs throughout the Sonoran Desert and extends into the Mojave Desert and also into the northern edge of the thorn forest. Its greatest abundance and best development are in the northern half of the Sonoran Desert. In Arizona it is characteristic of coarse outwash slopes and bajadas. Farther south it exhibits a complete reversal of habitat and occurs only on level plains with a coarse loam or sandy soil. In the thorn forest it is found only on the sandy soil of alluvial bottoms. It has a wide distribution in Baja California and is frequently seen there in pure stands.

LITERATURE

SHREVE, EDITH B. Factors governing seasonal changes in transpiration of *Encelia farinosa*. Bot. Gaz. **77**: 432–439, 1924.

Forchammeria Watsoni (Capparidaceae) JITO

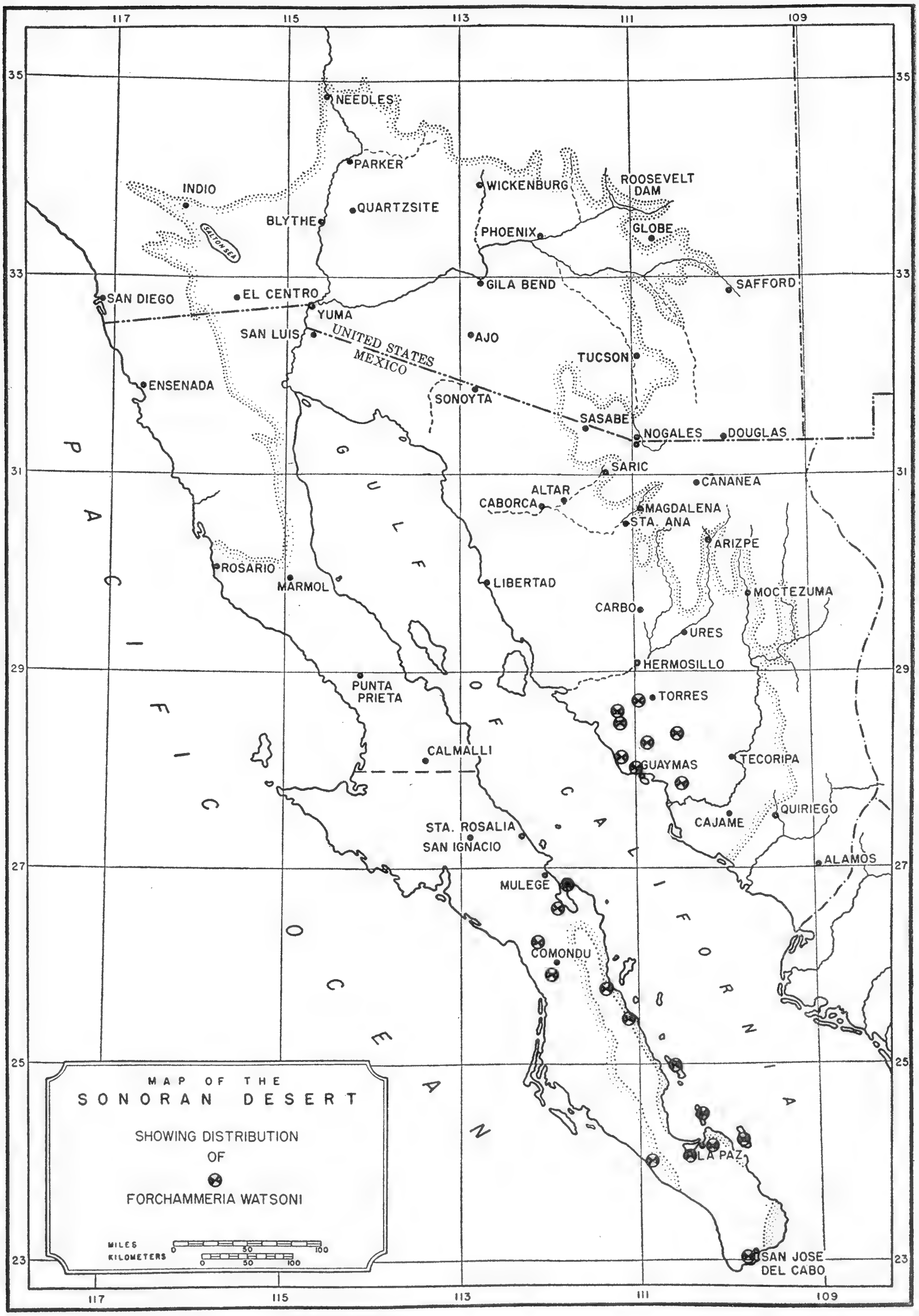
(Map 7)

This tree reaches a height of 12 to 15 m. and has a compact, rounded crown of dark green foliage (pl. 36). The thickness of the trunk is somewhat greater than the size of the tree would suggest. There are almost no dead limbs, and very few dead branches or twigs. The leaves are thick and coriaceous and are retained throughout the driest months. A general defoliation occurs at flowering time in March and April. *Forchammeria* is not a tree of arroyo margins, but grows with *Olneya* and *Cercidium* on the open desert south of La Palma and Torres, Sonora. The wood is very light in weight and burns so quickly that it is regarded as worthless for fuel. Samples of the wood taken in March showed a moisture content ranging from 47 to 60 per cent. In all the particulars that have been mentioned, except leaf texture, this tree departs so widely from the common characteristics of desert trees that its abundance here is a remarkable phenomenon.

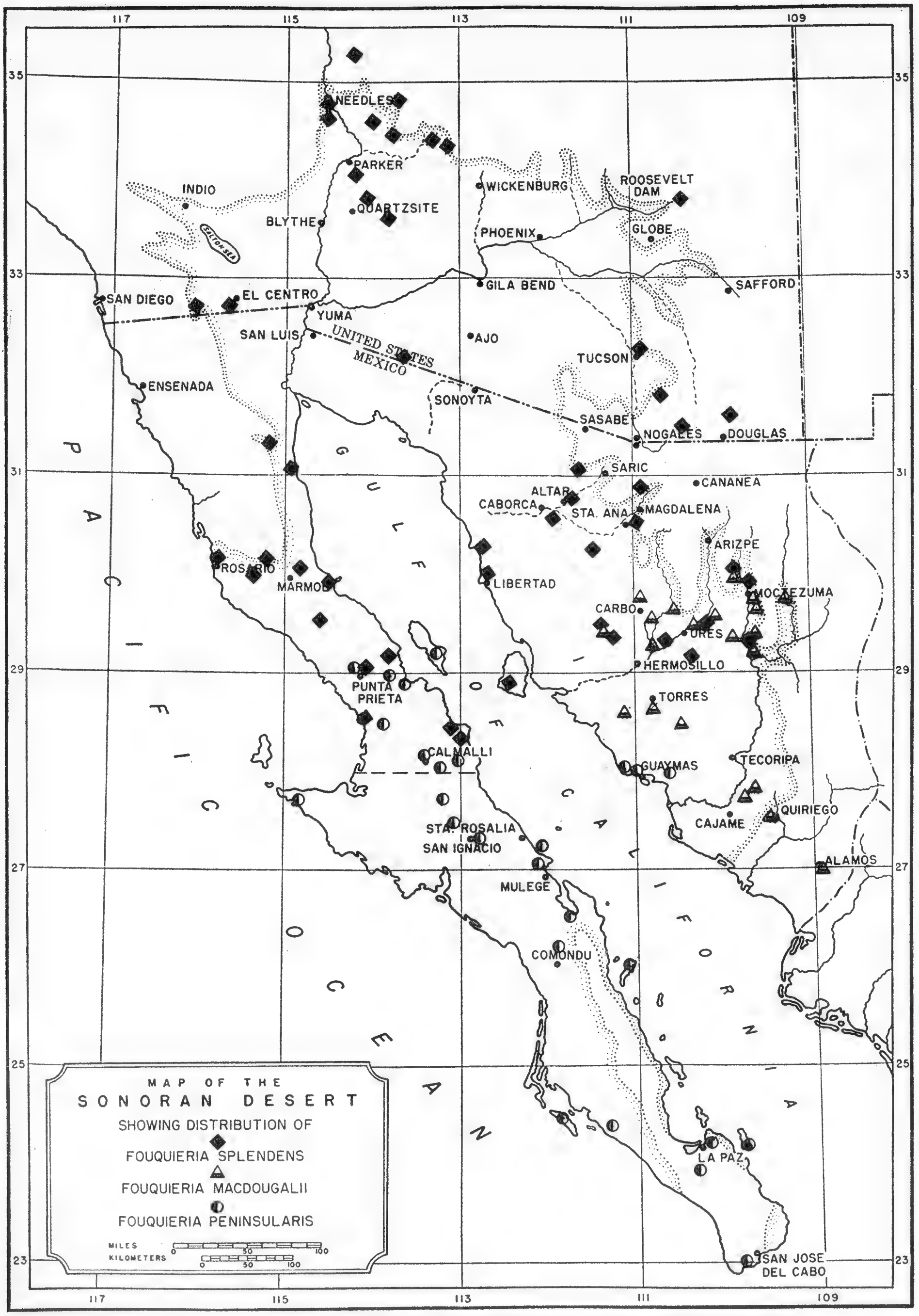
Fouquieria splendens (Fouquieriaceae) OCOTILLO

(Map 8)

The ocotillo is a plant of very distinctive appearance, which has been aptly described as suggesting "a loosely held group of wands." The branches arise from a short crown and grow to a length of 3 or 4 m., usually without forking; they are nearly straight, and the majority of them stand at an angle of more than 45° to the surface of the ground. The successive regions of growth in a long branch may be easily distinguished, and the diameter increases from 1 cm. at the end to as much as 5 to 7 cm. at the base. Shoots of recent growth are dark red, those of the preceding year are light gray with dark longitudinal markings, and the older parts of the stem are dark gray with frequent splits in the bark, revealing the light green layers of tough inner bark mentioned below. Elongation of the stems takes place only during the summer rainy period. The leaves on newly grown shoots have stout petioles about 1.5 cm. long. An elongation of the mechanical tissue of the petiole ends on the lower side of the leaf, near the base, as a small spine. When the leaf falls, it is the blade only which drops, and the petiole remains



MAP 7. Distribution of *Forchammeria Watsoni*



MAP 8. Distribution of *Fouquieria splendens, F. Macdougalii,* and *F. peninsularis*

as a slender spine from 1.5 to 2.5 cm. long. The leaves on older parts of the shoot are sessile and are borne in clusters from greatly shortened branches axillary to the spines. Leaves appear only after moderately heavy rains, either in winter or in summer, and the period of their persistence is determined by the duration of the rains. It may happen that there is such a distribution of wet periods as to bring forth five or six crops of leaves during the year. The foliage of *Fouquieria* is highly mesic in appearance, the leaves being thin, smooth, dark green, and with few of the structural features associated with arid conditions, except the depth of the chlorenchyma. The leaves are 1.5 to 4 cm. long and 0.5 to 1.5 cm. wide. *Fouquieria* is the only nonsucculent perennial of the region which can be propagated by cuttings.

The flowers of *Fouquieria* are borne in terminal racemes at the close of the winter rainy season. The light, thin-winged seeds are formed in great abundance and are readily disseminated by the wind. They germinate readily at the opening of the summer rainy season, and immense numbers of seedlings may be found in favorable localities late in July. From many thousands of seedlings, not more than two or three survive until the following summer.

The range of *Fouquieria splendens* slightly exceeds the limit of the Sonoran Desert throughout southern California and southwestern Arizona. Small colonies or single plants occur in many localities on the mountains which overlook the northern edge of the desert. In the Santa Catalina Mountains it occurs at 1800 m., and throughout the desert-grassland and encinal of southeastern Arizona it occurs on south exposures between 1500 and 1800 m. In many localities it is abundant on limestone at higher elevations and absent from neighboring soils founded on other types of rock. In the Swisshelm Mountains, in southeastern Arizona, it reaches the highest recorded altitude for the United States at 2100 m. These higher occurrences carry the continuity of distribution from the Sonoran to the Chihuahuan Desert.

In Baja California *F. splendens* is abundant at desert levels on the Gulf coast as far south as latitude 28°, and on the Pacific coast it extends from the desert boundary near Rosario southward nearly to the Vizcaíno plain. In southern Baja California *F. splendens* is absent and its place in the landscape is taken by *F. peninsularis*. In Sonora *F. splendens* is abundant north of latitude 29°, extending from the shores of the Gulf to the hills bordering the valley of Río Moctezuma. Here again there are many isolated occurrences of the plant far above the desert level. South of Río Sonora this species is infrequent, and it has not been observed south of the vicinity of Torres. In this region *F. Macdougalii* is the dominant member of the genus, but it does not take the place of *F. splendens* in the physiognomy of the vegetation.

Throughout most of its range *Fouquieria splendens* is most abundant on the shallow soil of rocky slopes or coarse outwash slopes. On the broad plains of the Lower Colorado Valley it occurs infrequently in the nearly pure stands of *Larrea*. When colonies of it occur in the *Larrea* plains, they are invariably found to be occupying sites with unusually rocky soil, derived from small volcanic emergences. In all parts of the desert with more than 100 mm. of rain, *Fouquieria* is absent from fine-textured soils and habitats subject to sheet flooding. In the drier parts of the desert it is frequent on finer soils and is occasionally found on sand. The root system of *Fouquieria* is shallow and wide-spreading, much like that of the cacti, and its optimum situation seems to require quick wetting and penetration in rainstorms, combined with good aeration at all times.

In the various parts of its range *F. splendens* differs considerably in height, number of stems, and amount of branching of stems, as well as in density of stand and rate of

growth. The largest plants are found in regions where the number of individuals is smallest, namely, in the driest part of the range on both sides of the head of the Gulf of California. A height of 10 m. is attained by many individuals in this region, with great variation in the number of stems, the largest of which have a diameter of 12 to 15 cm. On the coarse outwash slopes leading down to Bahía San Rafael, in Baja California, there is a very open stand of *F. splendens* in which all the individuals are from 6 to 10 m. in height, with very stout stems, commonly branched near the summit, with sinuously curved dependent ends. This is one of the finest stands of the plant in the Sonoran Desert, and the age of the individuals is probably much greater than in somewhat similar stands in areas of greater rainfall.

In the Arizona Upland *Fouquieria* commonly reaches a height of 3 to 6 m. In a representative group of 40 plants examined near Tucson, the average number of stems of all lengths was 25. In this region the stems are nearly straight, and branching is infrequent except on the largest plants. The stoutest stems are conspicuously more slender than in the plants of lower and drier areas, seldom exceeding 6 to 8 cm. in diameter. The amount of elongation in a single season can be easily determined by locating the nodelike places in the stem at which growth has been arrested and an inflorescence formed. Only a few of the stems on a single plant grow in length in a given season, but all of them increase in diameter and undergo surface changes. In the youngest growth the epidermis is mainly intact, the color dark red, and the spines long, slightly curved, dark red, and sharp. After 2 or 3 years the surface and spines become weathered, the epidermis cracks, and the formation of ridges of bark begins. At this time begins the segregation of subepidermal layers of unspecialized cells in which the lumen becomes filled with resin. As the stem advances in age, the layers of resinous tissue become thick and stout and envelop the entire stem in overlapping layers. The cracks in the epidermis and bark reveal the greenish resinous layers, the tough texture of which resembles the chitinous tissues in the joints of large crustaceans. These layers play an important role in protecting the stem from too great or too sudden loss of moisture. At the age of 5 to 6 years the stem has greatly changed from its early appearance, and the spines have become brittle or have weathered to half their original length. All these indications make it easy to distinguish a young, vigorously growing plant from an old, inactive one.

The heaviest stands of *Fouquieria* are found above 1000 m. along the upper edge of the desert and in hills just above the desert. All these stands occupy slopes gently inclined to the south or southwest and with a coarse soil filled and covered with rock fragments. The height of the plants is from 2 to 3 m., the number of stems is from 10 to 15, and the appearance of the stem surface indicates young plants and active growth. In all such stands the plants are so closely spaced that it is impossible to walk freely between them.

Literature

Humphrey, R. R. Thorn formation in *Fouquieria splendens* and *Idria columnæris*. Bull. Torrey Bot. Club **58:** 263–264, 1931.

——— A study of *Idria columnaris* and *Fouquieria splendens*. Amer. Jour. Bot. **22:** 184–207, 1935.

Shreve, Forrest. The establishment of desert perennials. Jour. Ecol. **5:** 210–216, 1917.

——— Die Fouquieriaceae. Pflanzenareale, ser. 3, no. 1, pp. 3–4, map, 1931.

Franseria deltoidea (Compositae)

(Map 9)

In spite of its perennial habit, the stems of *Franseria deltoidea* are slender and brittle, like those of many of the annual composites. Innumerable branches spring from the base and grow in such erect positions as to keep most of the foliage well above the soil surface. The compact crown is made up of many small leaves as well as a smaller number of full-sized ones from 1.5 to 2 cm. in length. Throughout its life the plant carries a large percentage of dead branches and leaves, which are shed only as a result of weathering. During the rainy seasons the plant is covered with large green leaves, which assume a grayish color with age. Very light rains give rise to a large number of small leaves. The fruits are spiny and produced in large numbers after both summer and winter rains. The plant is relatively short-lived. *Franseria deltoidea* occurs only on soil with a content and covering of coarse rock fragments. It is rarely found on sandy soil, and its local distribution is exactly complementary to that of *F. dumosa*.

Franseria deltoidea is found throughout the northern part of the Sonoran Desert and is not known beyond its boundaries. It is infrequent in Baja California and is not found in Sonora south of Río Sonora.

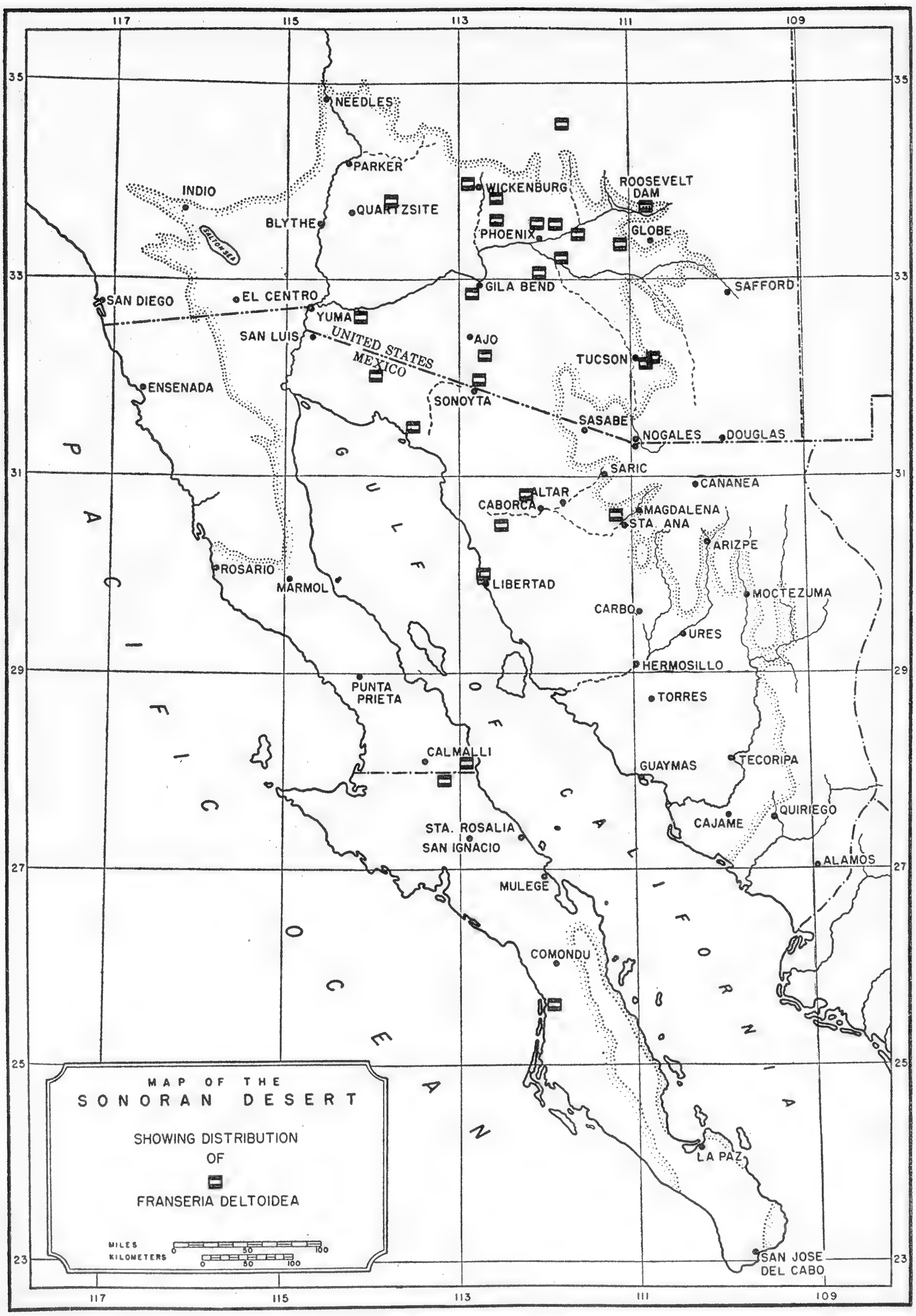
Franseria dumosa (Compositae) BURRO WEED

(Map 10)

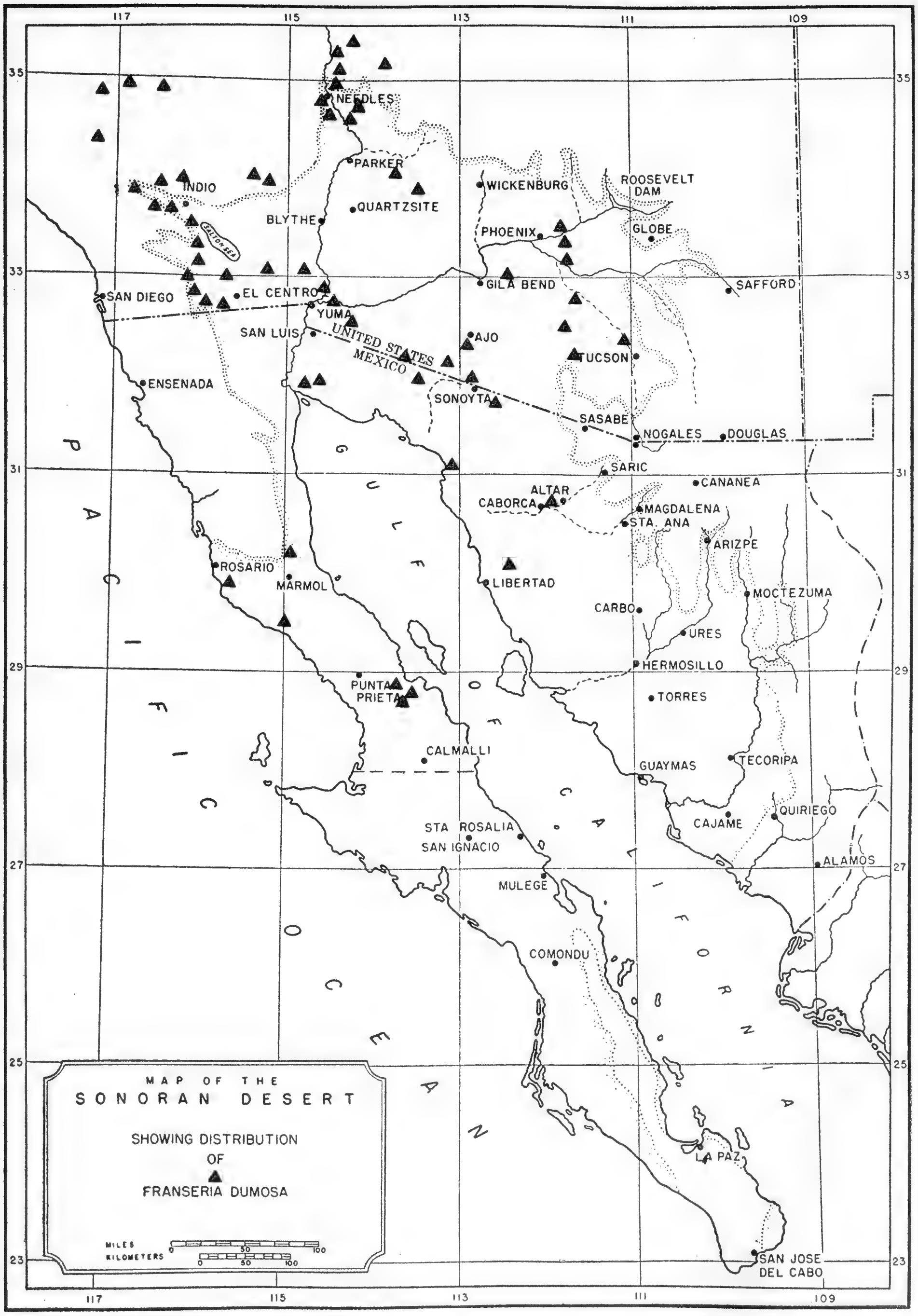
Franseria dumosa is the commonest plant in the most arid part of the Sonoran Desert (pl. 37). This small, gray suffrutescent perennial covers the floor of every valley from the eastern Mojave Desert south to the Río Magdalena, but is local in its occurrence above 600 to 700 m. On the plains near the head of the Gulf of California, on either sand or fine-textured soil, it occurs in open stands, either without associates or accompanied by very widely spaced plants of *Larrea*. In the same region it also occurs on extremely barren slopes and on sand dunes, where the individuals are few but large and well developed.

The plants of *Franseria dumosa* are roughly hemispherical, branching at the ground and consisting of an intricate maze of slender stems. The leaves are small and deeply divided and are so dry that it is often difficult to decide whether they are alive or in the first stages of desiccation. In the late spring a large percentage of the leaves die, change to a light fawn color, and either fall or remain attached to the plant for many weeks. The youngest leaves are the most likely to survive, and form a dense cluster at the end of the twig, where growth is quickly renewed after rainfall. The fallen fruits are covered with spiny processes, which improve the chances that the fruit will lodge in a spot favorable for germination. Under favorable conditions the growth of young plants is rapid and early accompanied by the development of a root from 5 to 15 times the length of the stem.

Franseria dumosa ranges north to Death Valley, southern Nevada, and southwestern Utah. It extends south along the Gulf in Baja California as far as Bahía Los Angeles and in Sonora as far as Tiburón Island. It has not been observed in southern Arizona above an elevation of 800 m.



Map 9. Distribution of *Franseria deltoidea*



Map 10. Distribution of *Franseria dumosa*. Also extends north to Death Valley, southern Nevada, and southwestern Utah.

Holacantha Emoryi (Simarubaceae) CRUCIFIXION THORN

(Map 11)

The leafless, green-stemmed *Holacantha* bears some resemblance to *Cercidium microphyllum*, but its habit is somewhat more erect and its ultimate branches are stouter (pl. 35, fig. 1). It is found as an individual tree or as a group probably having a common root system. It never forms pure stands, but is often fairly abundant as an associate of *Larrea*. The scattered colonies never extend more than a few kilometers and are widely separated by areas from which the tree is absent. Its occurrence is limited to outwash plains along the northern edge of the Sonoran Desert. It has been found in a few localities in extreme northern Sonora and is known from several localities in the Mojave Desert. The deeply divided leaves are found on seedlings and very small plants, but never appear on the new growth of mature trees. The fruits are borne in large clusters, and each seed is encased in a very heavy capsule. There is no mechanism for the release of the seeds, and the clusters remain on the tree until they are broken off by wind and the capsules have become gray and weathered. In the natural course of events it is at least 5 to 7 years after the maturing of a seed before it reaches the ground. Germination is further delayed by the thickness of the capsule wall, and can be hastened only by filing through it. When this is done, the seeds germinate readily, with a high percentage of viability. The seedlings at once develop a deep taproot, and grow rapidly if given an adequate water supply.

Idria columnaris (Fouquieriaceae) CIRIO

(Map 12)

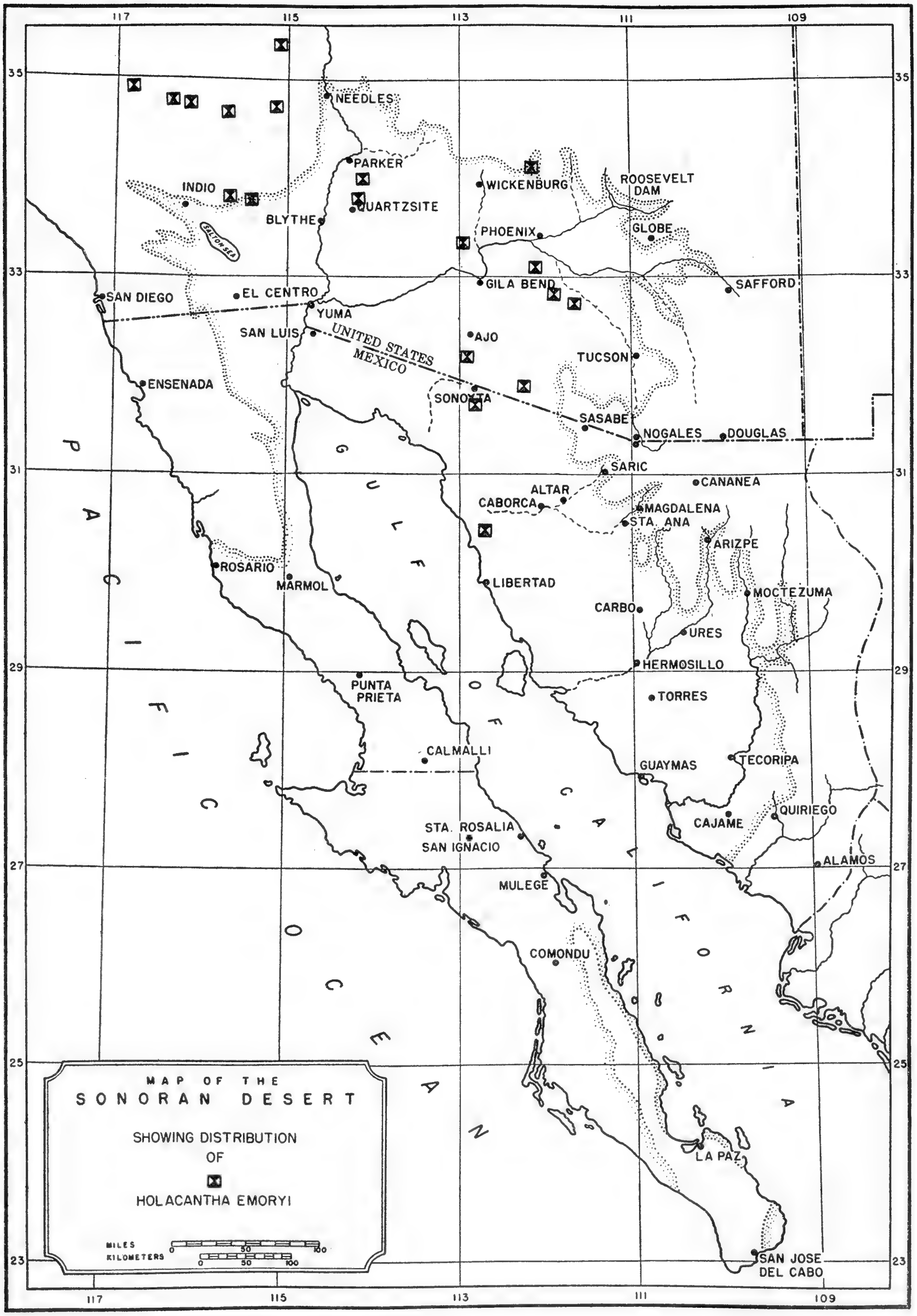
Idria ranks without rival as the most bizarre plant of the Sonoran Desert (pls. 23, 32). In fact, it is one of the most striking woody plants in the flora of North America. Its vegetative parts as well as its flowers indicate clearly its affinity with *Fouquieria*. In spite of its bulk, the trunk of *Idria* strongly suggests a single stout and erect branch of *Fouquieria splendens*. In mature trees the basal diameter of the trunk is 50 to 60 cm., or exceptionally as much as 75 cm. In many individuals the trunk tapers gradually from the base; in others it increases in diameter to a height of about 1 to 2 m. and then tapers gradually. The extreme top of the tree, from 6 or 8 m. to the tip, maintains a more uniform diameter of 6 to 12 cm. The trunk is brownish gray and covered by a smooth series of epidermal layers which are heavily permeated with mechanical tissue. The trunk is usually single to the top, but is sometimes branched. A wholly distinct type of short, slender branch is also borne on the lower part of the trunk. This type has a horizontal position, is repeatedly branched, and bears leaves but never produces flowers. The branches of the latter type arise from the trunk at regularly spaced intervals on great spirals, as if conforming to a very precise form of phyllotaxy.

LITERATURE

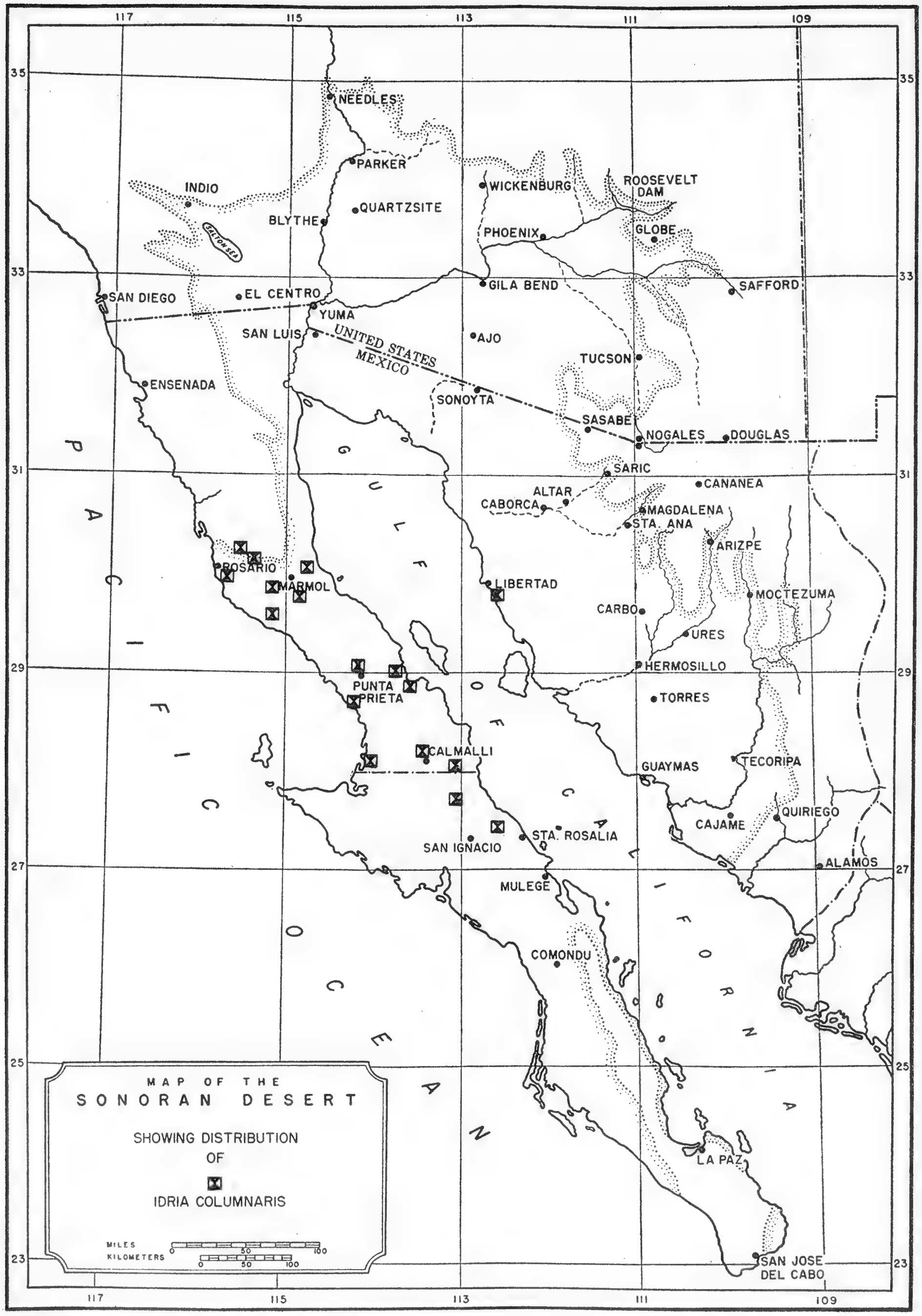
See under *Fouquieria*.

Ipomoea arborescens (Convolvulaceae) PALO SANTO

The palo santo, or morning-glory tree, occurs infrequently north of the Río Sonora along streamways, and becomes increasingly abundant toward the south. It is commonly



MAP 11. Distribution of *Holacantha Emoryi*. Also extends into Chihuahua and Zacatecas.



Map 12. Distribution of *Idria columnaris*

10 to 12 m. high and has a very open crown of ascending branches. The trunk is stout, but both trunk and stems taper rapidly. The large, mesic leaves are borne during the summer rainy period, and the conspicuous white flowers appear on the bare trees from December to March. It is a tree of relatively rapid growth.

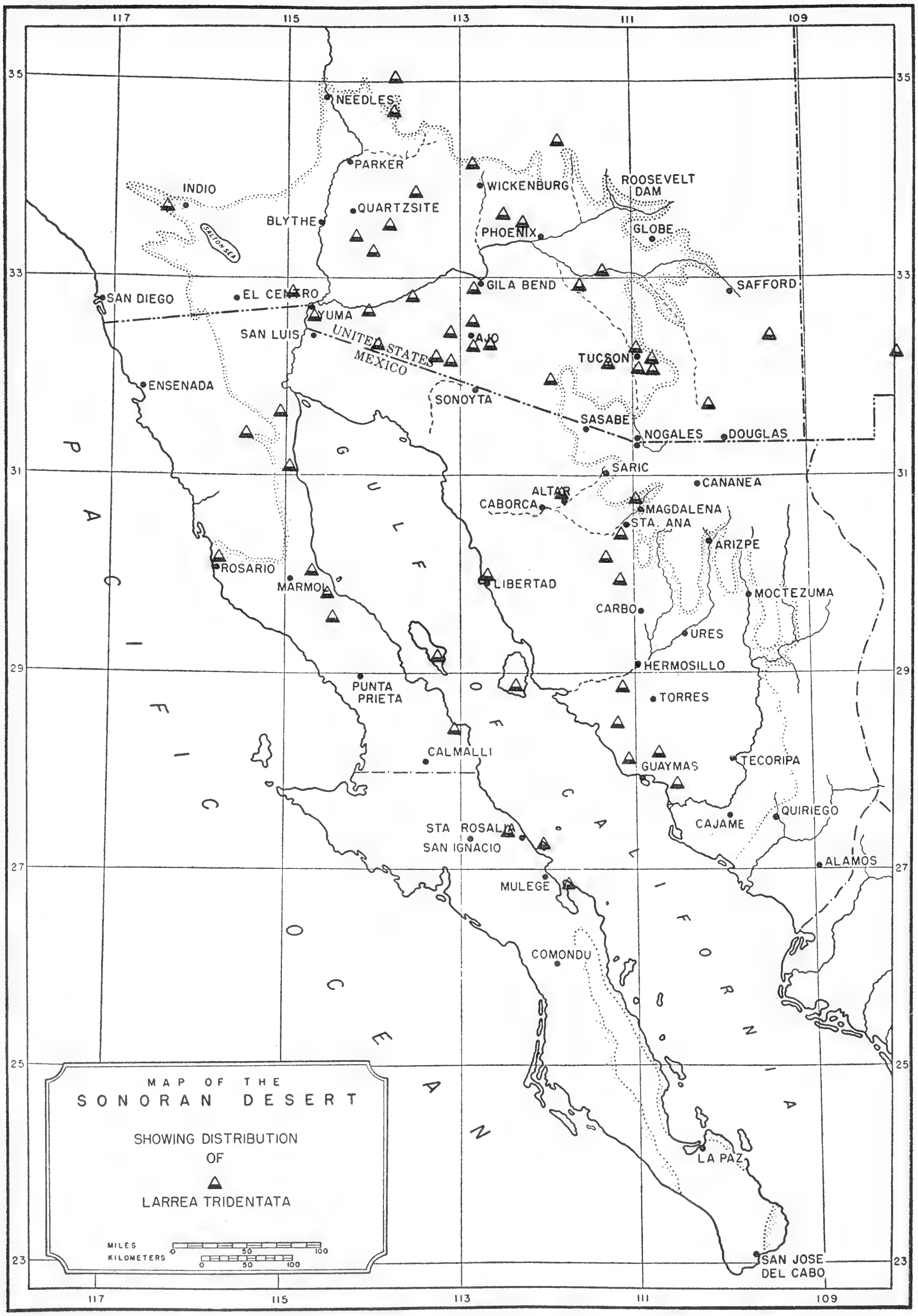
Larrea tridentata (Zygophyllaceae) — Creosote bush

(Map 13)

Larrea is one of the most abundant and widespread shrubs of the Sonoran Desert, and is equally prominent in the vegetation of the Chihuahuan Desert, the Mojave Desert, and a small part of the Great Basin Desert. It ranges from elevations below sea level in Death Valley to 2625 m. in the mountains of Zacatecas. It persists in regions in which 12 months frequently pass without precipitation, and, irrespective of differences in the seasonal distribution of rainfall, occurs in all sections of the desert and invades the edges of grassland and encinal areas in some of which the annual precipitation is about 500 mm. It grows on deep alluvial soil, on the edges of alkaline flats, on sandy plains, and on the rocky slopes of volcanic hills. It is rarely found on granite slopes and is uncommon on granitic soils. Its adaptability to a wide range of conditions is greater than that of any other desert plant. Also its height, density of branching, size of leaves, and rate of growth are very unlike under different conditions, since it responds readily to an increased water supply. Near the edges of its range *Larrea* is restricted to well marked habitats, but throughout the center of the desert it is less restricted, and in the most unfavorable areas it is highly ubiquitous.

The northern limit of distribution of *Larrea* is in southern Nevada and southwestern Utah, where it follows approximately the contour of 1200 m. In New Mexico the northernmost colonies are near Socorro, but isolated individuals are found 18 km. southwest of Santa Fe at an elevation of 1700 m. In Baja California, it is confined to the eastern side of the northern mountains but extends across the peninsula to the ocean near Rosario. It extends south to the vicinity of La Paz and Todos Santos, being absent from the southern mountains. At its eastern limit in Sonora *Larrea* occurs in large or small isolated colonies, as is also the case in the belt which connects the ranges in the Sonoran and Chihuahuan Deserts. The southern limit on the coast of Sonora is about 12 km. southeast of Guaymas.

Mature individuals of *Larrea* consist of a group of slender branches growing vertically or obliquely from the crown of the root. There is no main branch, either in position or in size. Lateral branches are few below but abundant above, and all the branching is dichotomous. On the twigs there is a slightly elevated ring at each node, which is still recognizable after considerable thickening of the limb. Young plants are simple and graceful in form. With advancing age the crown thickens and the number of branches increases. Young branches usually have an erect position, but gradually bend down as additional branches are formed, through their own weight, through the impact of heavy rains, or particularly through the weight of snow. In very old plants the crown is 20 to 30 cm. thick and the number of branches well over 100. In such plants the largest branches are nearly horizontal and mixed with large dead ones, and the younger oblique and vertical branches carry the bulk of the foliage. The age of an individual is indicated by the size of the crown, and is greater than the age of any of the dead or living limbs. It is therefore impossible to estimate the greatest age which *Larrea* may attain, but probably it greatly exceeds 100 years.



Map 13. Distribution of *Larrea tridentata*. Also in Chihuahuan Desert, Mojave Desert, and part of Great Basin Desert.

The foliage of *Larrea* is well distributed throughout the crown of the plant, but is heaviest near the ends of the branches. Under the most favorable conditions the foliage is so light that the plant never casts a solid shadow. Under unfavorable conditions many of the leaves are shed, after turning from a deep olive green to a light brownish green. Under very unfavorable conditions tufts of foliage persist here and there on plants which are mainly bare of leaves. A leafless branch is not necessarily dead, but will die if conditions force it to remain leafless for many months.

The leaves of *Larrea* are bifurcated and vary greatly in size according to the moisture conditions at the time of their growth, ranging from 4 to 28 mm. in length. Young leaves which are arrested in growth by drought will usually resume growth on the return of favorable conditions. Under conditions which have not been well determined, the surface of the leaves is covered with a lac or varnish which makes them shiny and viscid. The leaves of *Larrea* are shed copiously during drought periods, but at least 10 to 20 per cent of them are retained during all but the most prolonged rainless periods. They are not winter-deciduous and are rarely injured by low temperatures except at the northern limit.

Flowers are borne sparingly or copiously near the ends of the youngest shoots, and appear after the rains which terminate a drought period, at whatever time of the year they may fall. The principal flowering period follows the late winter rains. The fruits come to maturity in about 6 or 8 weeks and open in a manner which causes some of the seeds to be shed immediately while others remain on the plant. Finally the slender pedicel of the fruit breaks and the entire crop falls to the ground beneath the parent plant. Owing to the lightness of the fruits and their hairy covering, they are blown about to a slight extent and washed away by rain to a much greater extent.

Like those of nearly all other desert perennials, the seeds of *Larrea* germinate in the warm, moist period of July and August. There is a notable scarcity of seedlings in the common stands of mature shrubs. On ground that has been cleared, raked, cultivated, or covered with new soil, the number of seedlings is large. The amount of growth during the first 2 or 3 years varies greatly in different individuals, so that 3-year-old plants may be from 2 or 3 cm. in height to 10 or 15 cm. On disturbed areas a very dense stand of young shrubs may persist until the tallest ones have reached a height of 60 to 80 cm., by which time there is high mortality among the repressed individuals, so that the resulting mature stand is very little denser than is commonly the case.

Literature

Runyon, E. H. The organization of the creosote bush with respect to drought. Ecology **15:** 128–138, 1934.

Shreve, Forrest. The edge of the desert. Yearbook Assoc. Pacif. Coast Geographers **6:** 6–11, 1940.

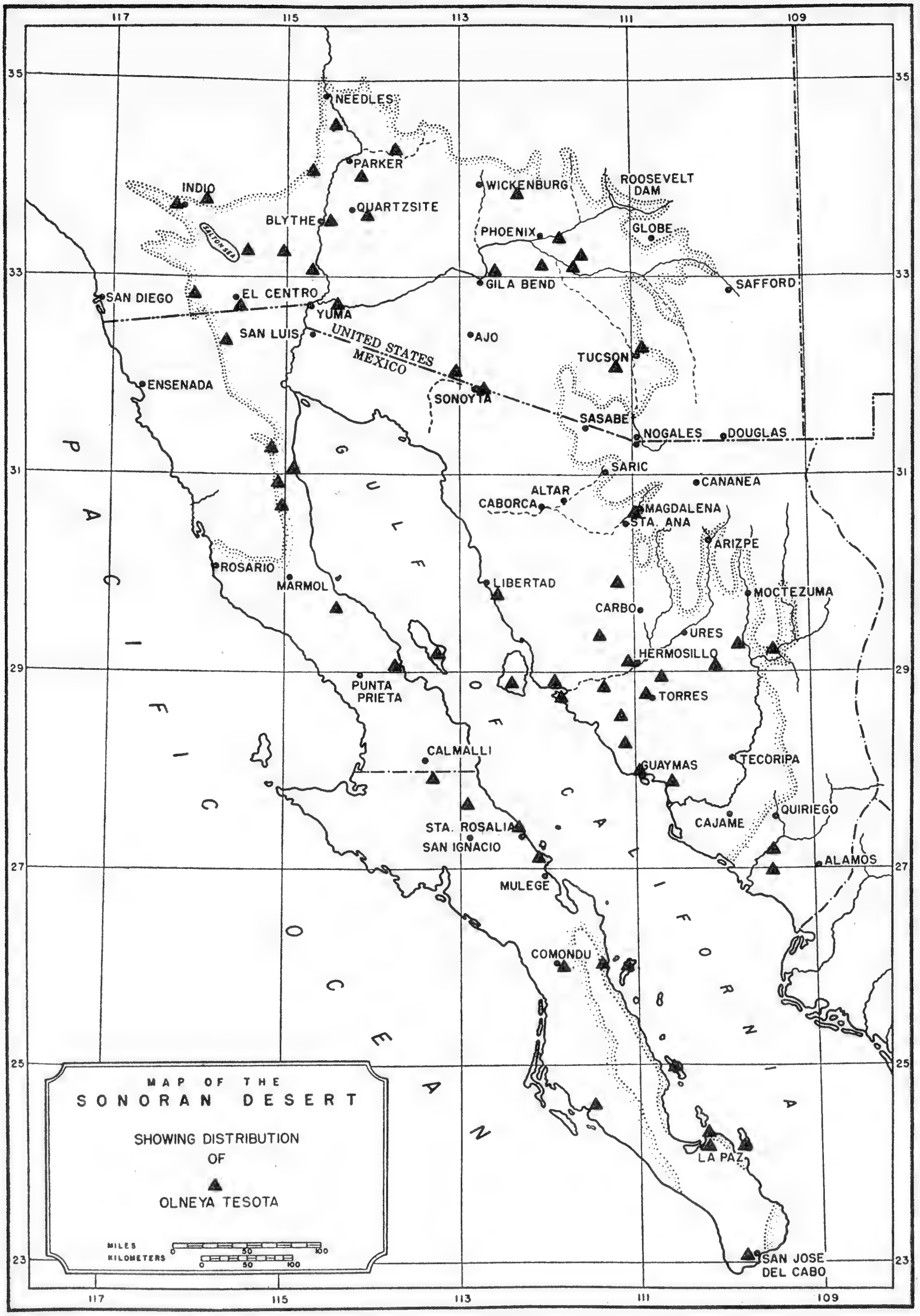
——— and T. D. Mallery. The relation of caliche to desert plants. Soil Sci. **35:** 99–112, 1933.

Spalding, V. M. Biological relations of certain desert shrubs. I. The creosote bush (*Covillea tridentata*) in its relation to water supply. Bot. Gaz. **38:** 122–138, 1904.

Olneya tesota (Fabaceae) — Ironwood. Tésota

(Map 14)

Olneya tesota is a leguminous tree belonging to a monotypic genus. It is most abundant in the parts of the Sonoran Desert with less than 200 mm. of rainfall. Even under very



MAP 14. Distribution of *Olneya tesota*

adverse moisture conditions it often reaches a height and bulk exceeding those of any other nonsucculent plant in the region.

The distributional limits of *Olneya* correspond closely to the outlines of the Sonoran Desert, but its occurrence is not continuous throughout that area. A few isolated colonies have been noted at short distances beyond the desert at its northern edge, and in the south it occurs in a few localities south of the Mayo River. In Baja California the tree is found throughout the length of the peninsula on the Gulf side but is rare or absent on the Pacific side. In the Arizona Upland *Olneya* occurs in numerous but sharply circumscribed areas, above the lowest plains and on outwash slopes or benches, where temperature inversion does not subject it to the lowest minimum temperatures of the coldest winter nights. In central Sonora it is very abundant near the coast and on the broad plains, but occurs only in scattered colonies along the eastern edge of the desert. The damage suffered by *Olneya* from exceptionally low winter temperatures indicates that they are important in limiting its northern distribution (Turnage and Hinckley, 1938).

The mature trees of *Olneya* have a single trunk or a group of trunks with the lowest limbs either well above the ground or prostrate on it. The main trunk is often surrounded by young upright branches, by suckers from the roots, and by dead trunks of various sizes. Almost every tree shows the loss of small limbs or even of large accessory trunks as a result of drought. Normally the crown is fairly dense, and vigorous trees throw a heavy shade. The leaves are compound, with 12 to 20 leaflets and a total area of about 350 sq. mm. The leaflets are thin and flexible, but the foliage is evergreen and falls in part only as a result of severe drought or heavy frost. In drought the leaflets fall without change of color. After frost the leaves die but do not fall for several weeks. Leafless living trees are seldom seen, and have been noted by the writer only between Ehrenberg and Quartzsite, Arizona, in June 1936.

Flowers appear in March, being very abundant in about 2 years out of 5, and almost wholly absent in the other years. It has not been possible to correlate the appearance of flower crops with the moisture or temperature conditions of the preceding months. The fruit is a short indehiscent pod, usually containing a single seed and very rarely more than two. The pods ripen from about the end of May to the middle of June and fall as soon as mature. The seeds are black, oval, about 8 mm. in length, and provided with a heavy, slightly waxy coat. Like all the other large, nutritious leguminous seeds, those of *Olneya* are eagerly sought by all the desert rodents. At night in season a continuous crackling sound may be heard under every tree as the rodents remove the seeds from the pods. The principal factor favoring the germination of the remaining fraction of the seed crop is the occurrence of unusually early rain. The thin wax coating does not serve to delay the germination of the seeds, which takes place within a few weeks of their fall. A single rain may rupture the seed coat without providing the continued moisture needed for full germination. Large numbers of seeds with ruptured coats have been seen under trees in northwestern Sonora, together with a few in which the radicle and plumule had begun to grow. Although these seeds had been thoroughly dry for a fortnight, they were found to be capable of resuming the process of germination when placed in moist soil. All the seeds with merely ruptured coats that were tested were found viable, but only a few of the slightly more advanced ones with a dried radicle and plumule were capable of growth.

Olneya is readily propagated from seeds, but the number of natural seedlings and small plants in all parts of its range is extremely small. With a limited supply of water, greenhouse seedlings will reach a height of 15 to 20 cm. in the first year. Suckers and

vigorous young branches on trees in the open make a growth of as much as 20 cm. in a single season with good soil-moisture conditions. Nothing is known of the average growth performance of the tree or of its length of life.

The sapwood of *Olneya* is light yellow, and 2 to 4 cm. thick. The heartwood is dark brown and has the extreme hardness which gives the tree its English name. Rings of growth are discernible in both layers of wood, but are very narrow and greatly interrupted, and serve only as a record of the number of favorable seasons in the life of the tree.

The commonest cause of the death of large trees is a prolonged saturation of the soil, such as frequently occurs during the summer rains as a result of the clogging of former drainage channels and the spreading of the floodwater over areas which offer it no outlet. Small groves of dead trees are frequent along the western edge of the Plains of Sonora. The sapwood of dead trees is quickly consumed by termites, but the heartwood is not attacked. Groups of trees which have been dead for several years consist merely of the abbreviated heartwood skeleton, which withstands weathering for many years. The constant movement of wind-blown sand near the ground level slowly cuts the base of the skeleton until it is small enough to break.

LITERATURE

TURNAGE, W. V., and A. L. HINCKLEY. Freezing weather in relation to plant distribution in the Sonoran Desert. Ecol. Monogr. **8:** 529–550, 1938.

Pachycereus pecten-aboriginum (Cactaceae) HECHO

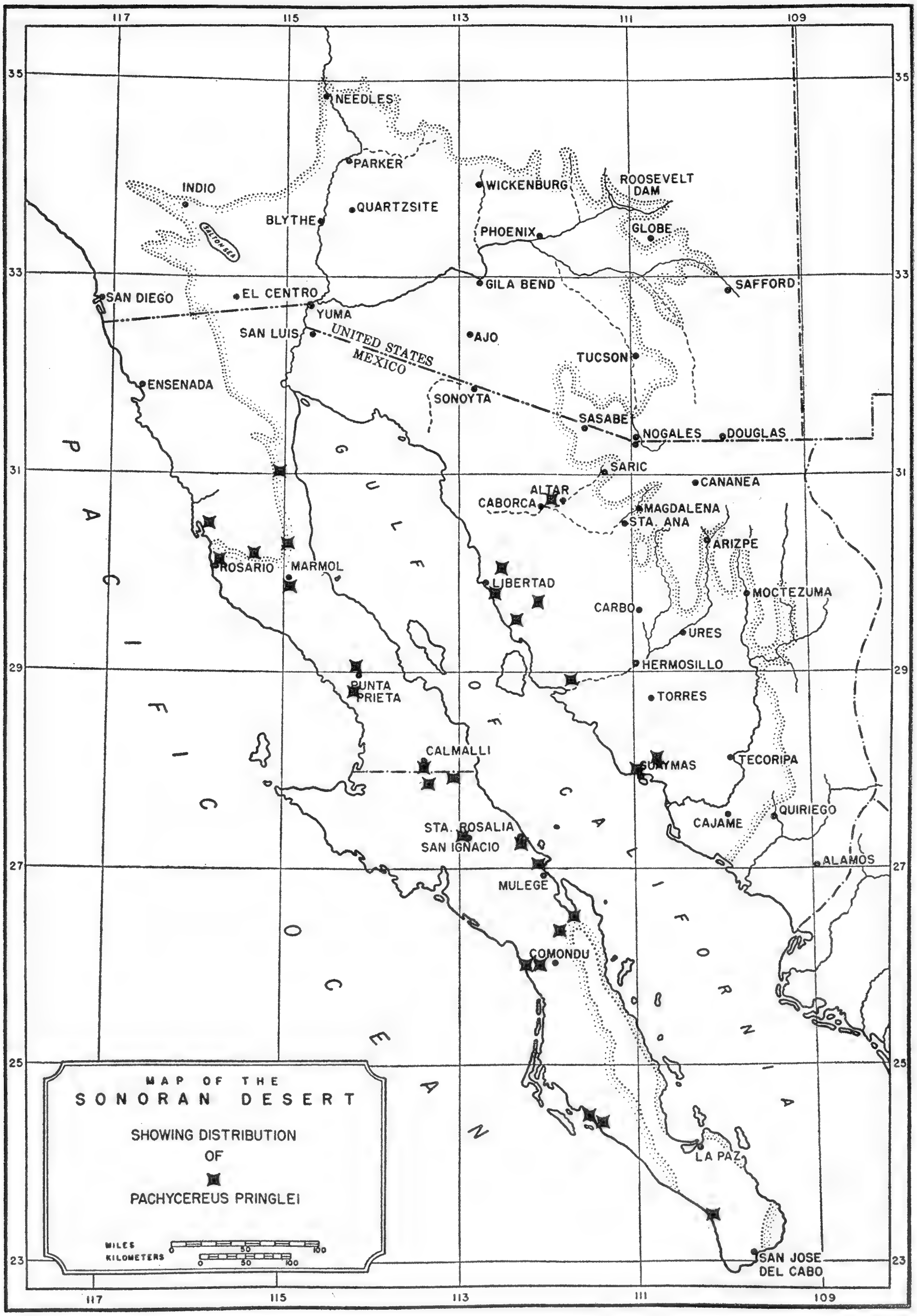
This stout columnar cactus reaches a height of 10 to 12 m. Its branches are numerous and sharply ascending. It is rare in the open desert, and its northernmost representatives are found in thick stands of trees and shrubs. *Pachycereus pecten-aboriginum* occurs sparingly in the southern part of the Plains of Sonora, but becomes abundant in the thorn forest of Sinaloa. The dry fruit is covered with strong, slender spines. The specific name of the plant refers to the use of the fruits as combs, a practice which is still very common.

Pachycereus Pringlei (Cactaceae) SAHUASO. CARDÓN

(Map 15)

In size and general form *Pachycereus Pringlei* is similar to *Carnegiea*, but the two can be readily distinguished at a distance. *Pachycereus* is more massive and more compactly branched, its center of gravity is nearer the ground, and the branches are inserted at a sharp angle rather than a sweeping curve.

Pachycereus Pringlei occurs almost throughout the desert areas of Baja California and near the coast in central Sonora, only slightly overlapping the range of *Carnegiea* and rarely growing in equal abundance with it. The northernmost occurrence of *Pachycereus* in Baja California is in the foothills west of Bahía San Felipe (latitude 31° N.), where it is very infrequent. On the Pacific coast its northernmost occurrence is about 40 km. north of Rosario. Southward from these localities it rapidly increases in abundance and is found from coast to coast in every area that has been visited below an elevation of about 700 m. In Sonora, *P. Pringlei* is abundant in a coastal belt about 50 km. wide, extending from Sierra Picú, northeast of Puerto Libertad, south to hills east



Map 15. Distribution of *Pachycereus Pringlei*

of Guaymas. A single isolated colony is known about 100 km. from the coast near Pitiquito. Throughout most of the range it occurs as isolated individuals or in very open stands associated with many other plants. Like those of *Carnegiea*, its heaviest stands are on coarse outwash slopes and low hills, but it is much more tolerant of sand and alluvial soil than is *Carnegiea*. The maximum of size and abundance, and the greatest catholicity of habitat, are on the Gulf coast of Baja California in the vicinity of Mulegé and Bahía Concepción. The only heavy stand observed in Sonora is on the outwash slopes overlooking the tidal flats near Empalme.

Young plants of *P. Pringlei* are slender at the base for many years, but increase greatly in thickness after formation of branches begins. The old branched individuals are massive, with the trunk reaching a diameter of 50 to 60 cm. and the branches a diameter of 30 to 40 cm. In favorable situations the plants often reach a height of 10 to 12 m. and produce from 5 or 6 to as many as 30 branches. It is only rarely that the sahuaso retains an upright posture with all its branches in erect position. They usually give the impression of having been vigorously battered by the wind and thrown out of balance by their great weight.

The longitudinal grooves of the stem are at first deep, but become more shallow with increasing age. In young plants the ridges are capped by a close-set series of areoles with white glochids. The glaucous green of the surface is marked by faint dark lines which run from the bottom of the groove to the apex of the ridge. On the trunks of old trees, a smooth gray bark replaces the green surface and there is little or no indication of the ridges, which have been flattened by the secondary thickening. The smooth, gray trunk vividly suggests the leg of an elephant. Higher on the old plants a rough bark is formed, gradually extending down from the tops of the ridges, on which the remaining glochids are now black.

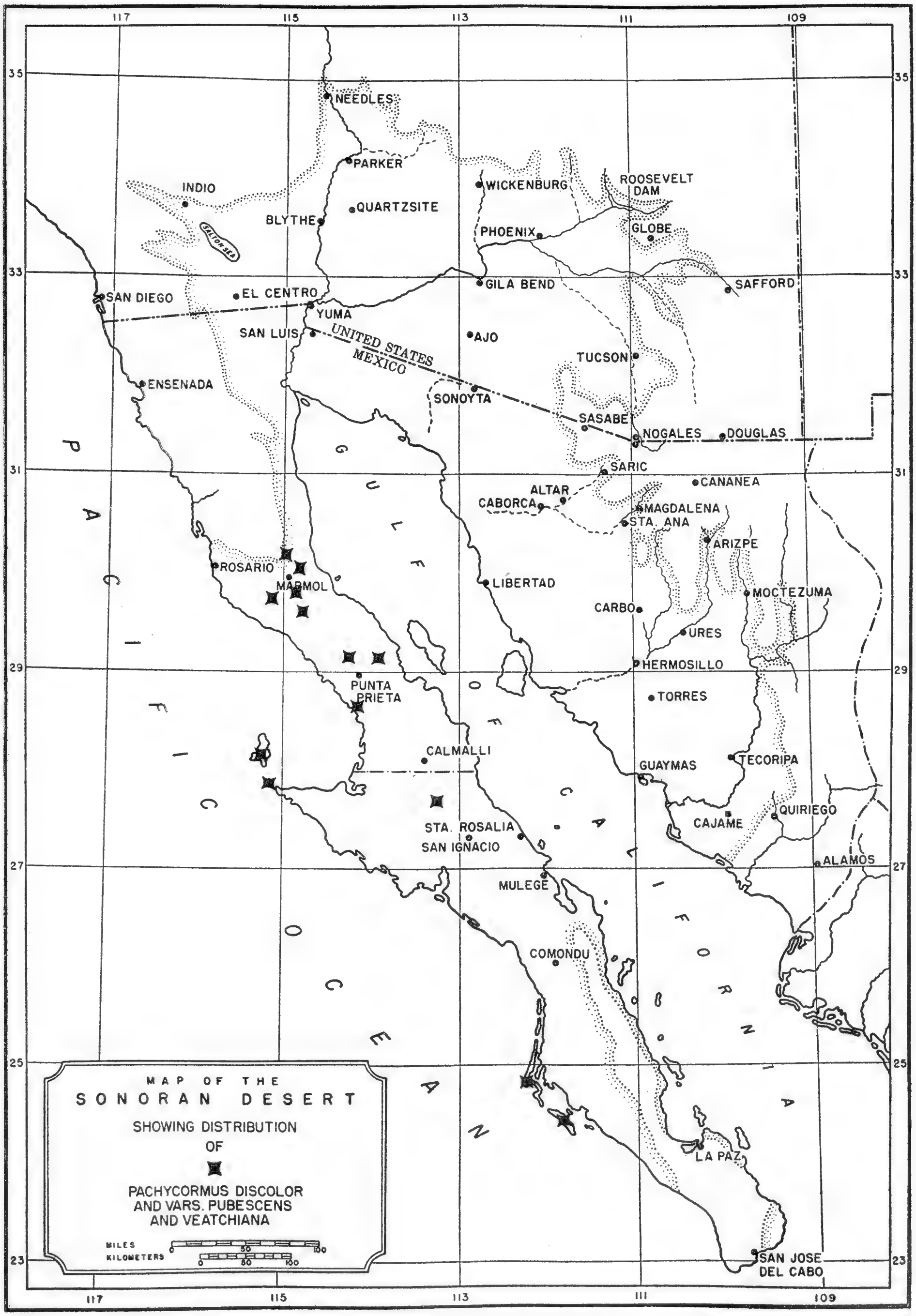
The skeleton of *P. Pringlei* is a cylinder of 12 to 15 ribs which are separate in the upper part of the trunk, but connected below by loose, open woody tissue in which there are longitudinal rows of small holes 1 to 2 cm. apart. In trunks 40 to 50 cm. in diameter the ribs are fused into a solid cylinder 3 to 4 cm. thick, but sometimes still show series of small holes 2 to 4 mm. in diameter, the last vestiges of the areoles. The basal part of the woody cylinder is about 15 cm. thick and occupies most of the cross section of the trunk, with only a small lumen at the center and a thin outer cortical layer.

The flowers of *P. Pringlei* appear in late March or early April, arising from the areoles just below the apex of the stem down to 30 or 40 cm. from the apex. The fruit is relatively dry at maturity and contains about 500 very small seeds, a large number of which are abortive. The features of germination and growth are much like those in *Carnegiea* so far as is known. In comparable stands of the two plants, the number of small individuals is commonly somewhat greater in the case of *Pachycereus*.

Pachycormus discolor (Anacardiaceae) — Elephant tree. Torote

(Map 16)

Pachycormus is one of the most striking and beautiful trees of Baja California; also it often assumes very grotesque forms (pl. 35, fig. 2). In all locations it has a trunk and limbs of exaggerated thickness, and near the Pacific coast it is usually prostrate and gnarled. In the interior the trees are upright and freely branched, usually with a clean trunk of 5 to 12 dm. between the ground and the lowest limbs. The trunk and limbs are covered with a smooth, light buff bark which exfoliates repeatedly during the life



MAP 16. Distribution of *Pachycormus discolor* and vars. *pubescens* and *Veatchiana*

of the tree. The dark green compound leaves are borne during the rainy seasons and shortly thereafter. The flowers are small and inconspicuous. A very stout-stemmed species of dodder infests the trees in rainy years and appears to be responsible for the death of many of the badly infested individuals. *Pachycormus* is found on rocky slopes and hillsides throughout the central third of the peninsula of Baja California. In some localities it is abundant, in others it is absent over large areas. Its best development and greatest abundance are in the hills near the drainage divide of the peninsula, but it extends down to the Gulf coast in several places and is known from Angel de la Guarda Island.

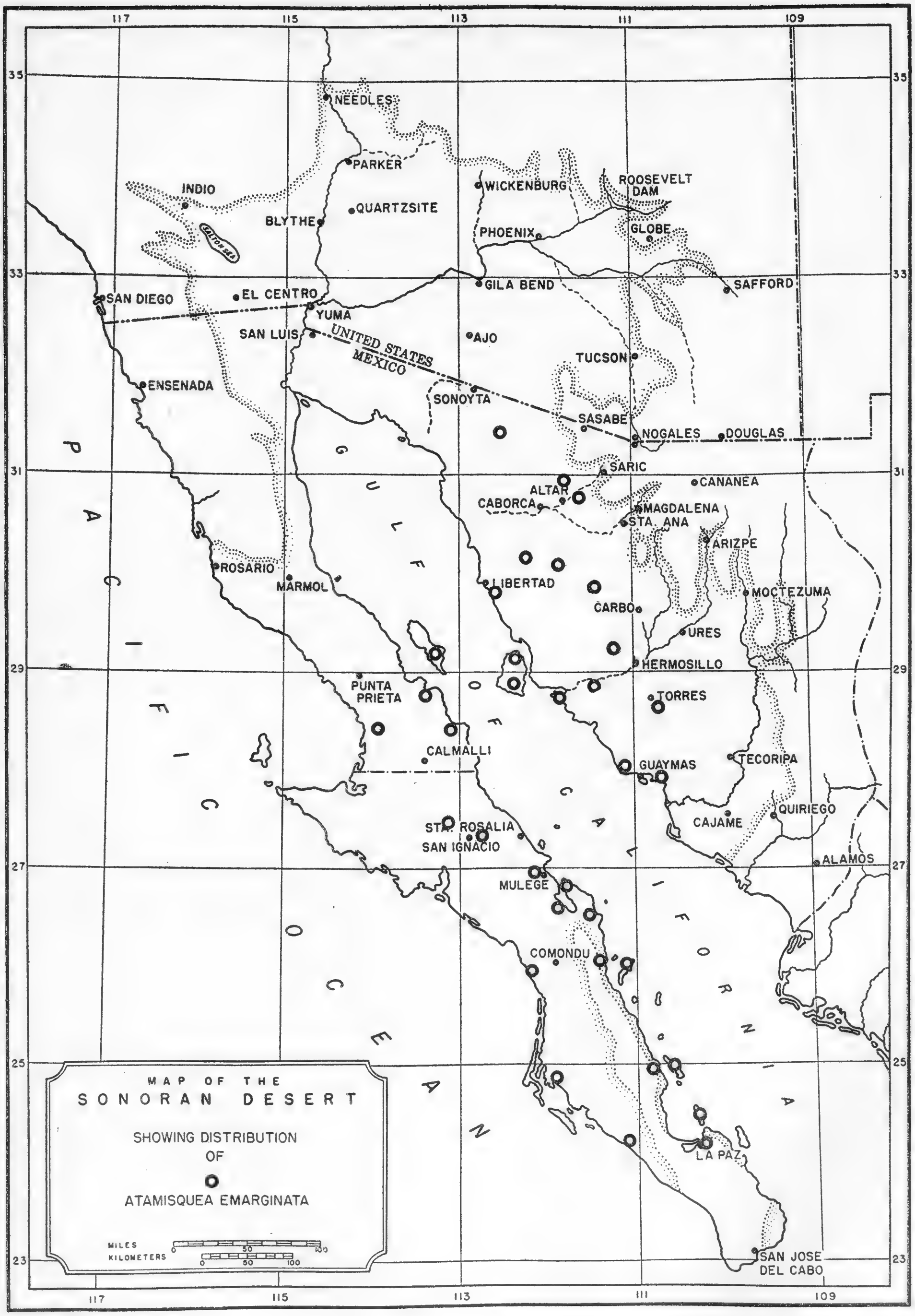
Piscidia mollis (Fabaceae)

This is a small tree, rarely exceeding 7 m. in height, with the irregular form and branching of an oak. It has an open crown and large, sericeous, trifoliolate leaves. There is considerable defoliation in the late spring, but the tree is never leafless. *Piscidia* is infrequent but conspicuous in the southernmost part of the Plains of Sonora, where it is confined to the eastern half of the area.

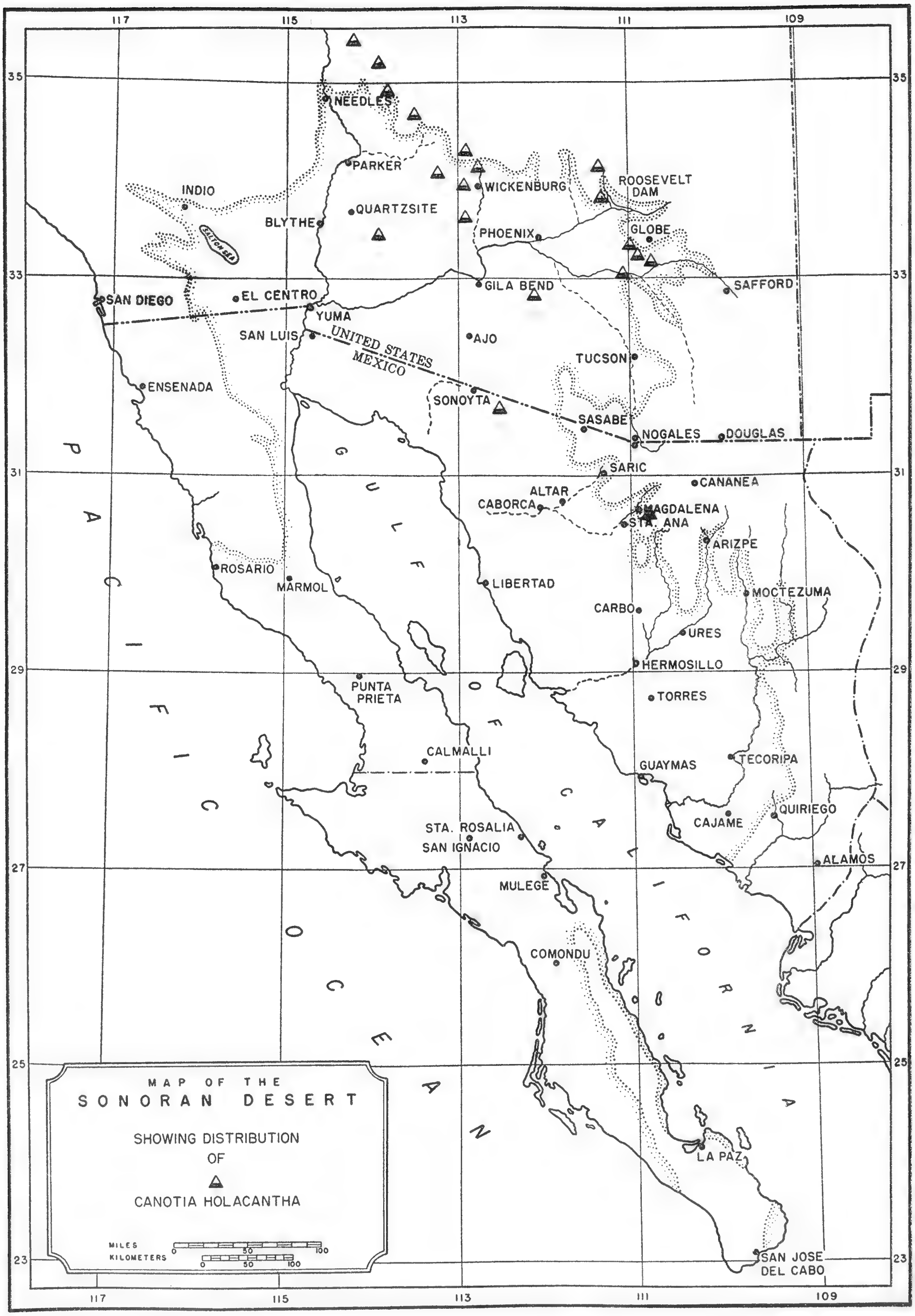
Pithecellobium sonorae (Mimosaceae) PALO JOCONO

A slender tree with a compact, narrow crown, often 8 m. in height. Single individuals are less common than close groups of small trees surrounding two or three large ones. The bark is light gray and beset with short, sharp thorns. The leaves are bipinnate, about 4 cm. long, and bear from 4 to 6 pinnae with very small leaflets 3 to 4 sq. mm. in area. This species of *Pithecellobium* is found only in the southern part of the Plains of Sonora, where its tall, narrow crown makes the scattered individuals conspicuous along the streamways.

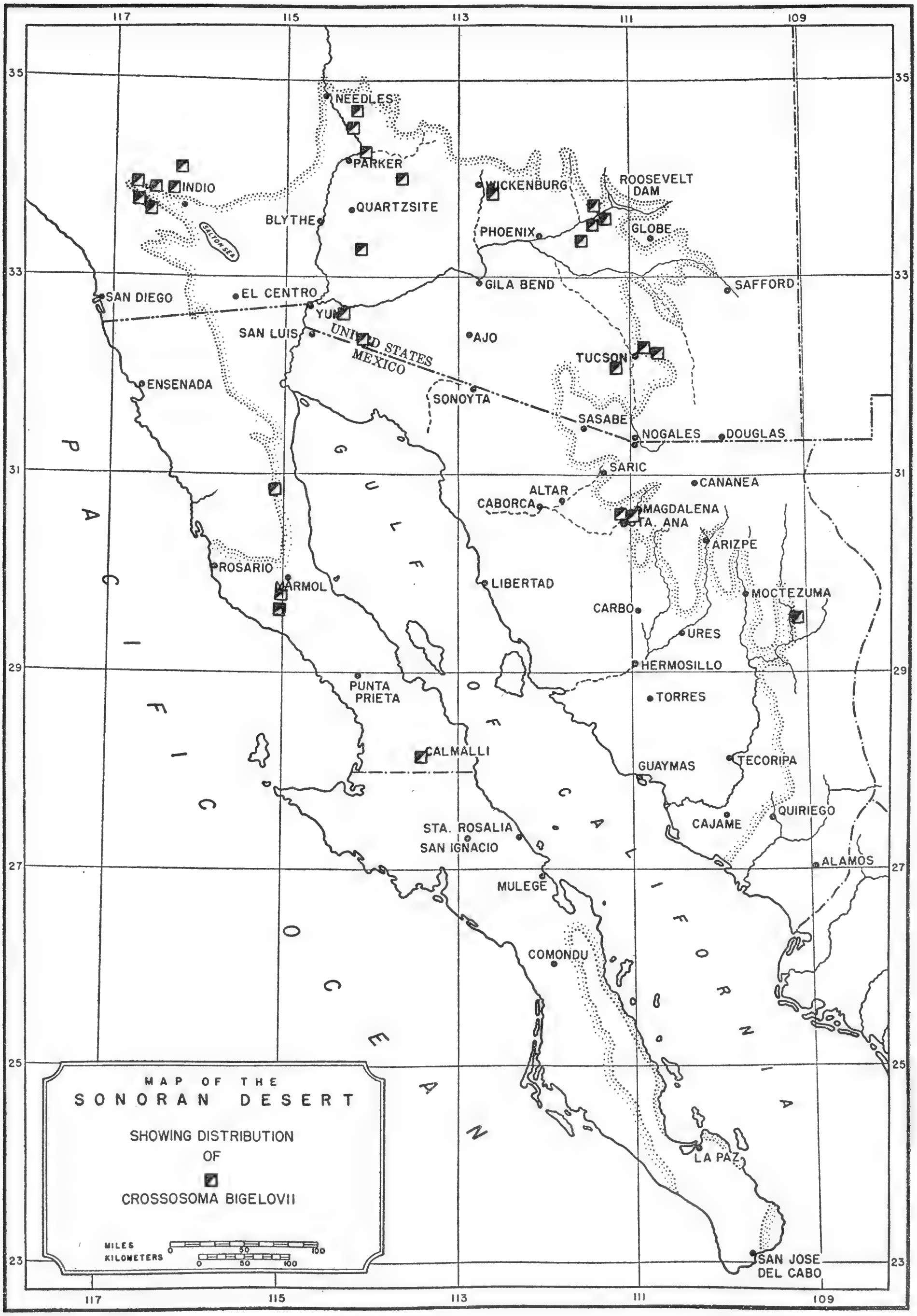
Maps 17 to 27 show the known distribution of species important in the make-up of the flora of the Sonoran Desert, but not described individually in the text.



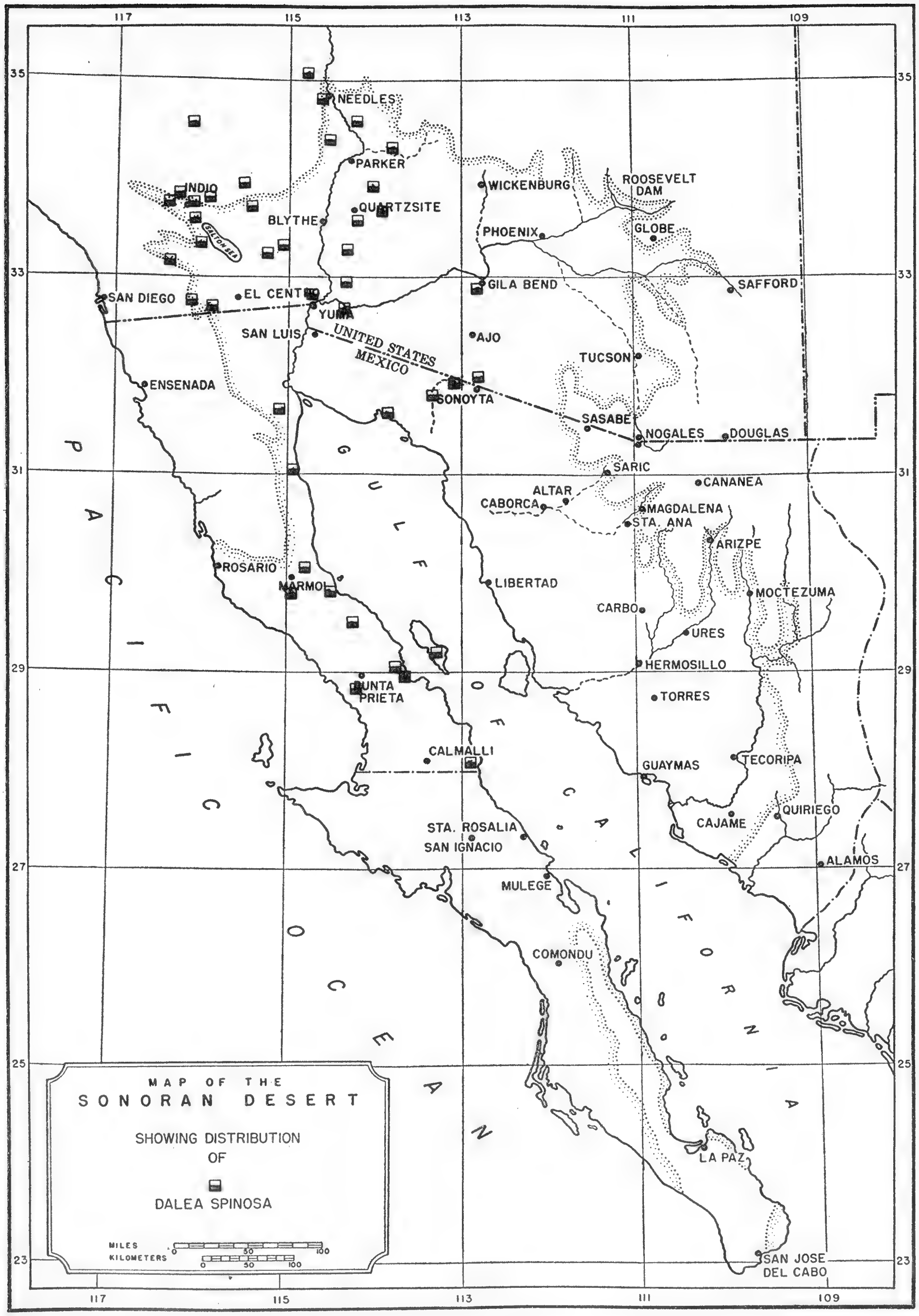
Map 17. Distribution of *Atamisquea emarginata*



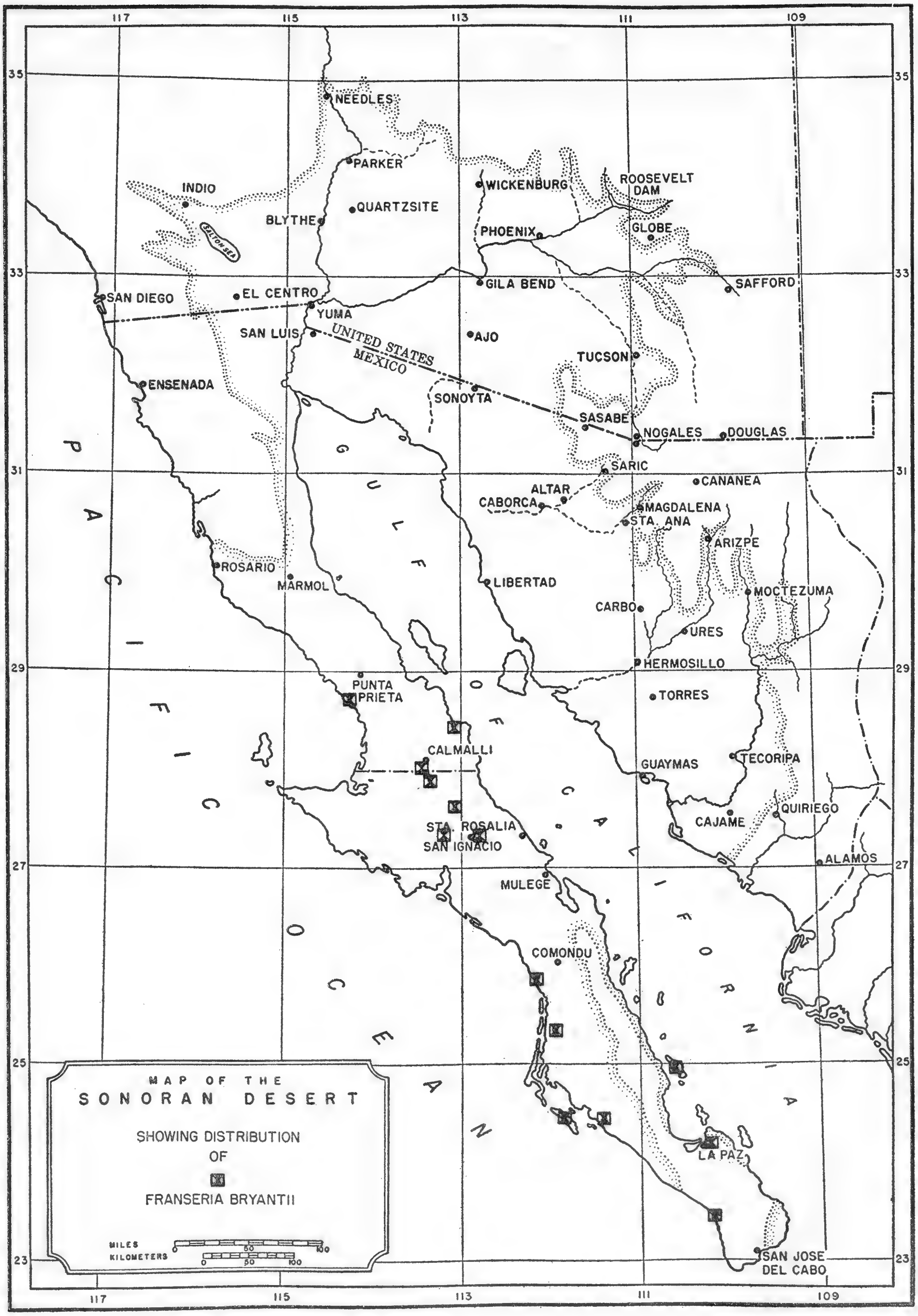
Map 18. Distribution of *Canotia Holacantha*



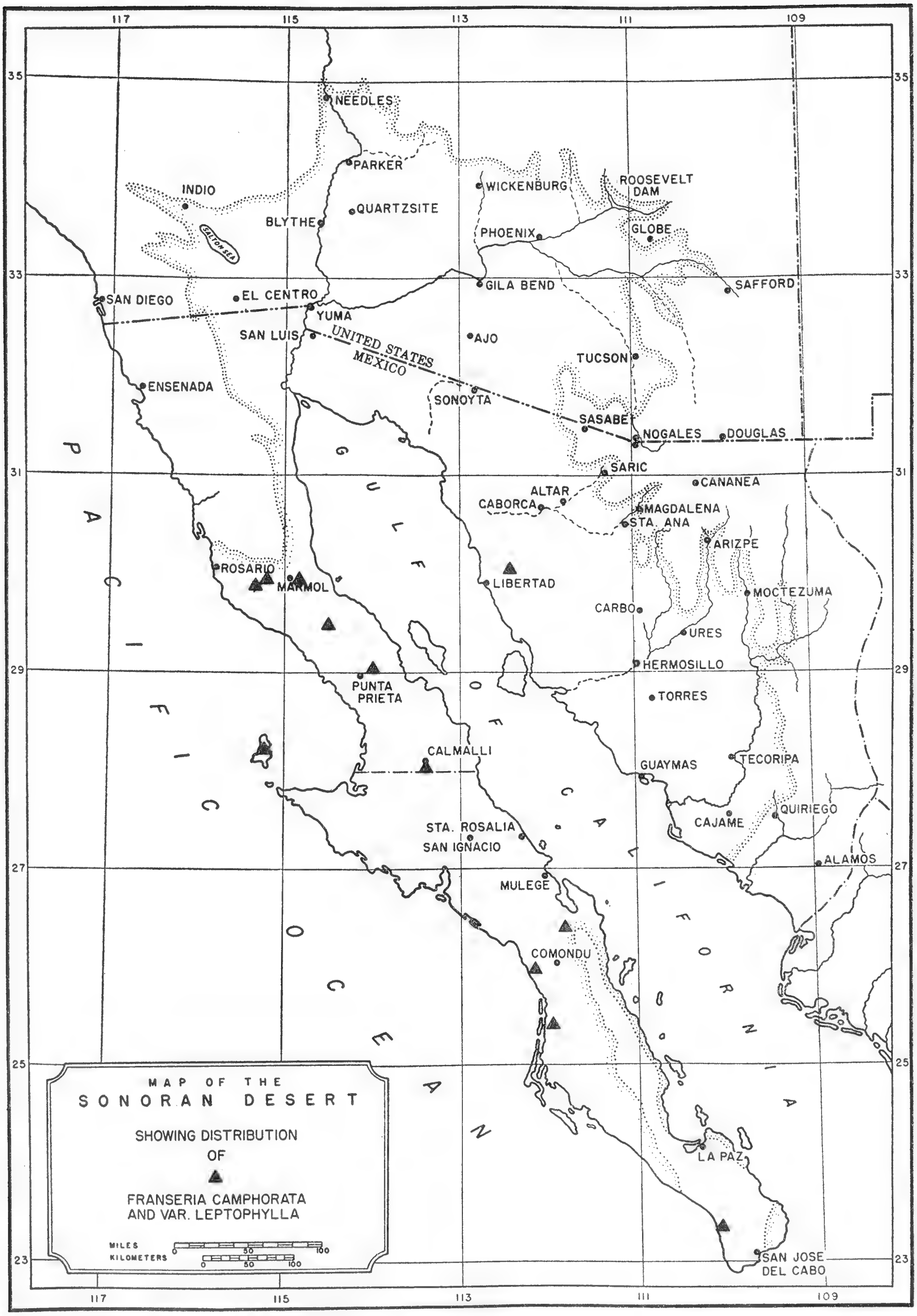
MAP 19. Distribution of *Crossosoma Bigelovii*



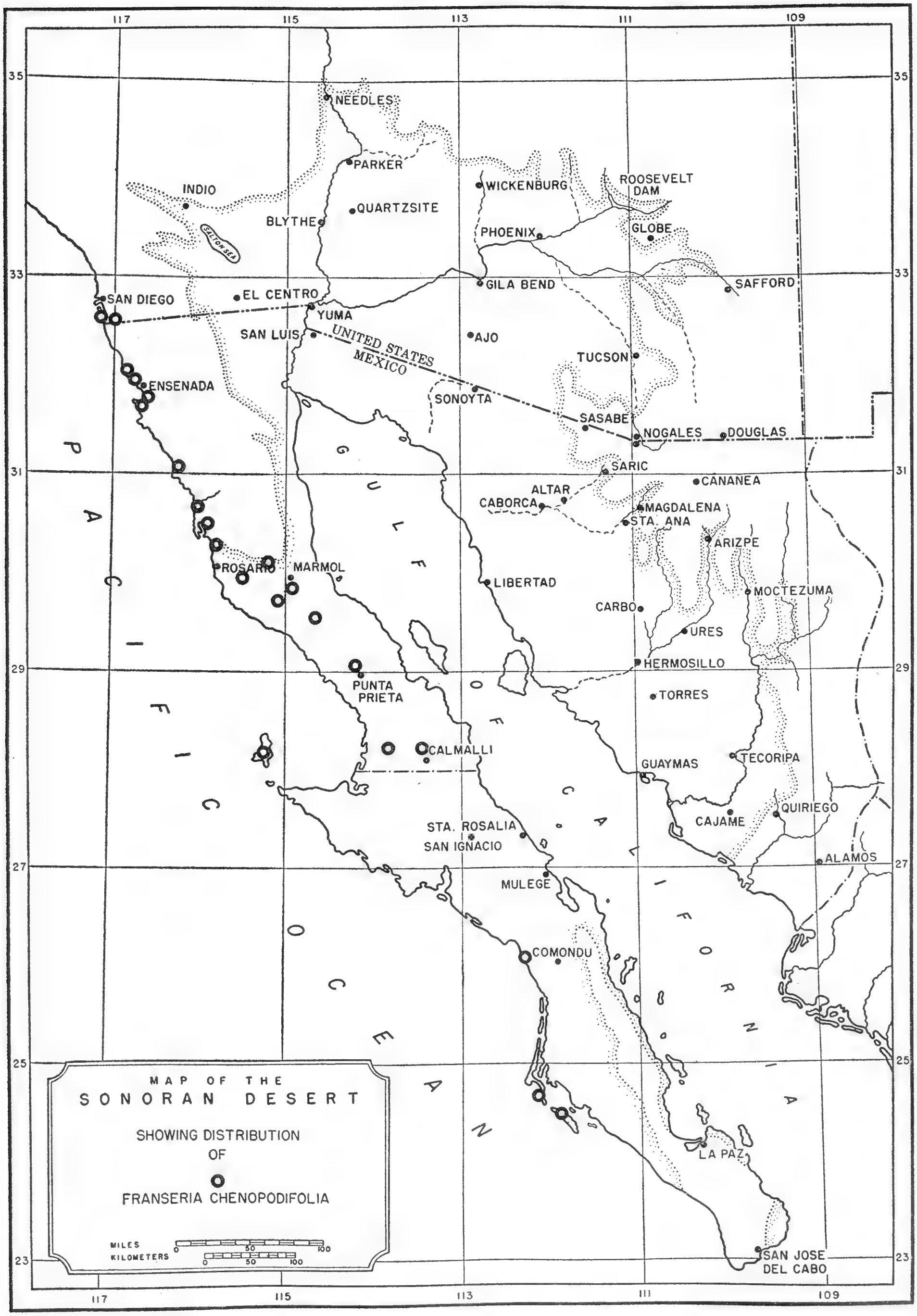
MAP 20. Distribution of *Dalea spinosa*



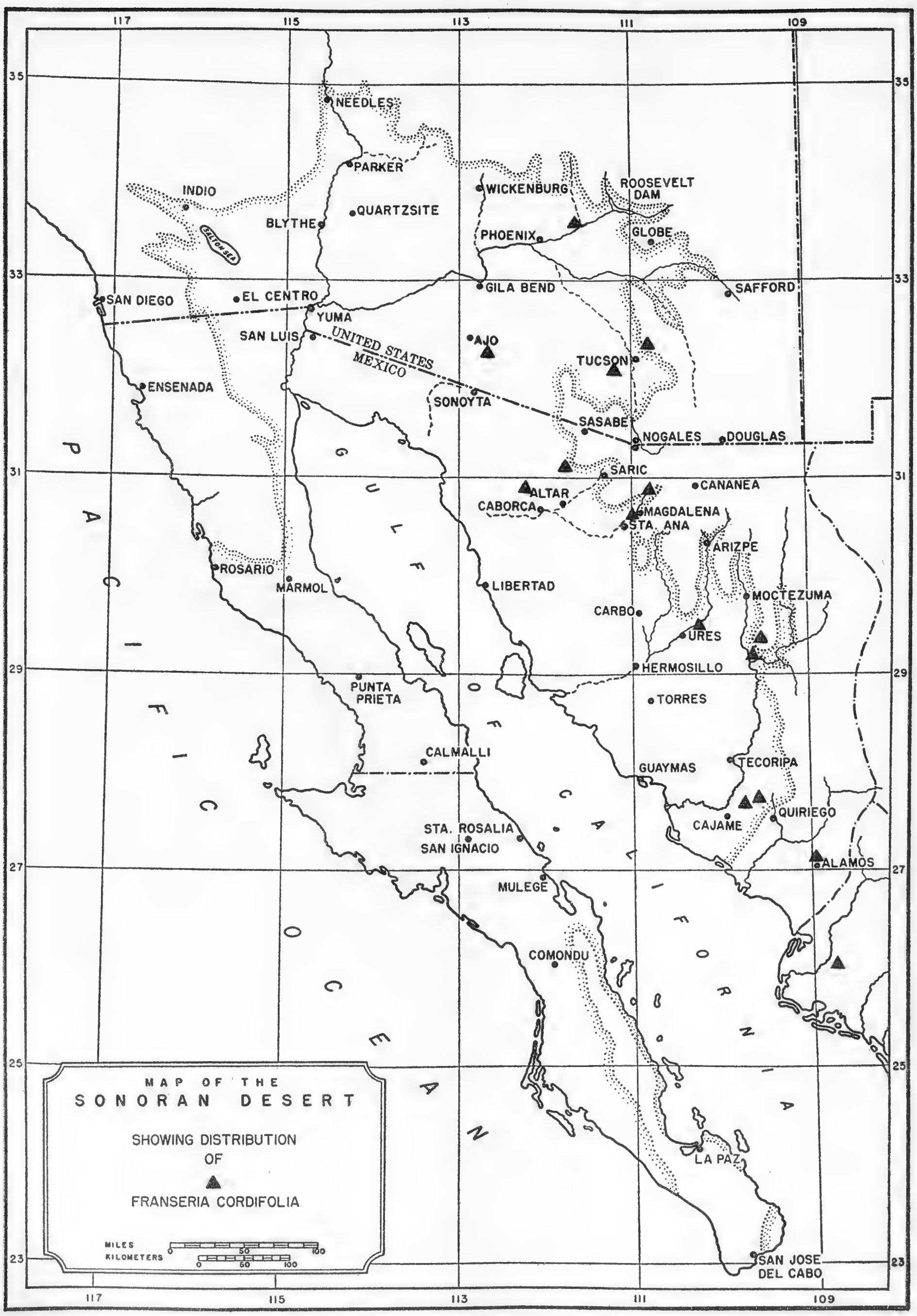
MAP 21. Distribution of *Franseria Bryantii*



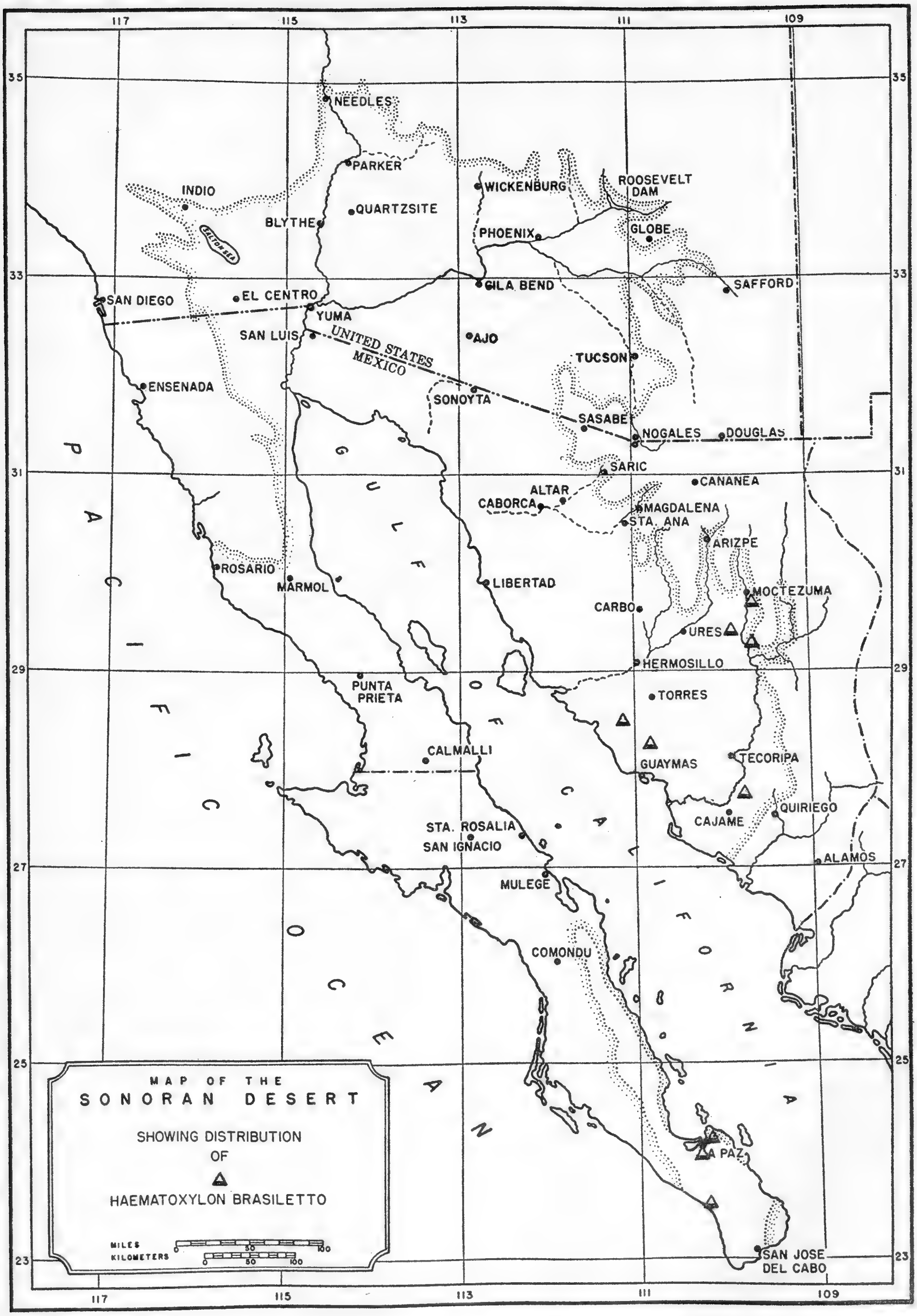
Map 22. Distribution of *Franseria camphorata* and var. *leptophylla*. Also on Guadalupe Island.



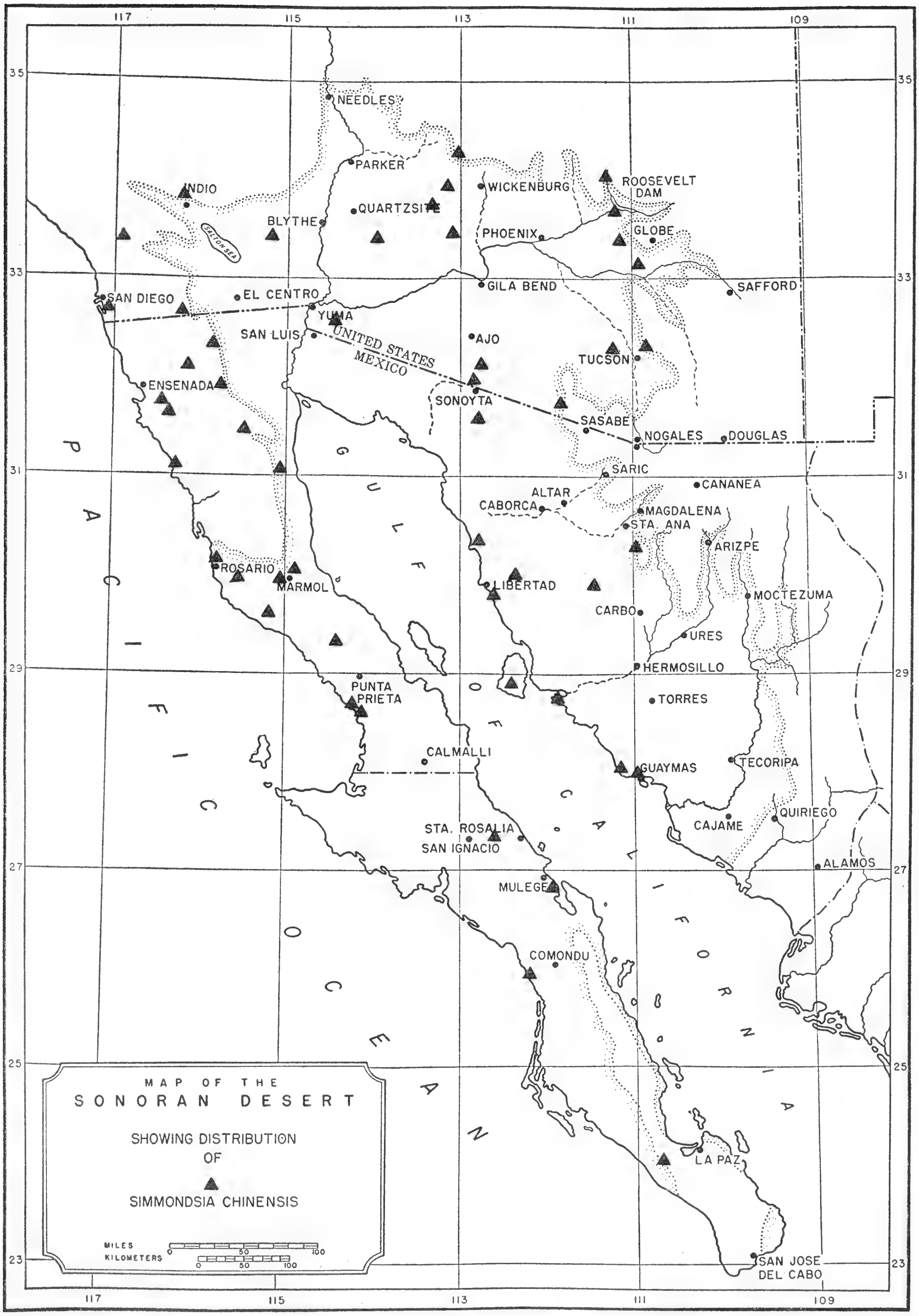
MAP 23. Distribution of *Franseria chenopodifolia*



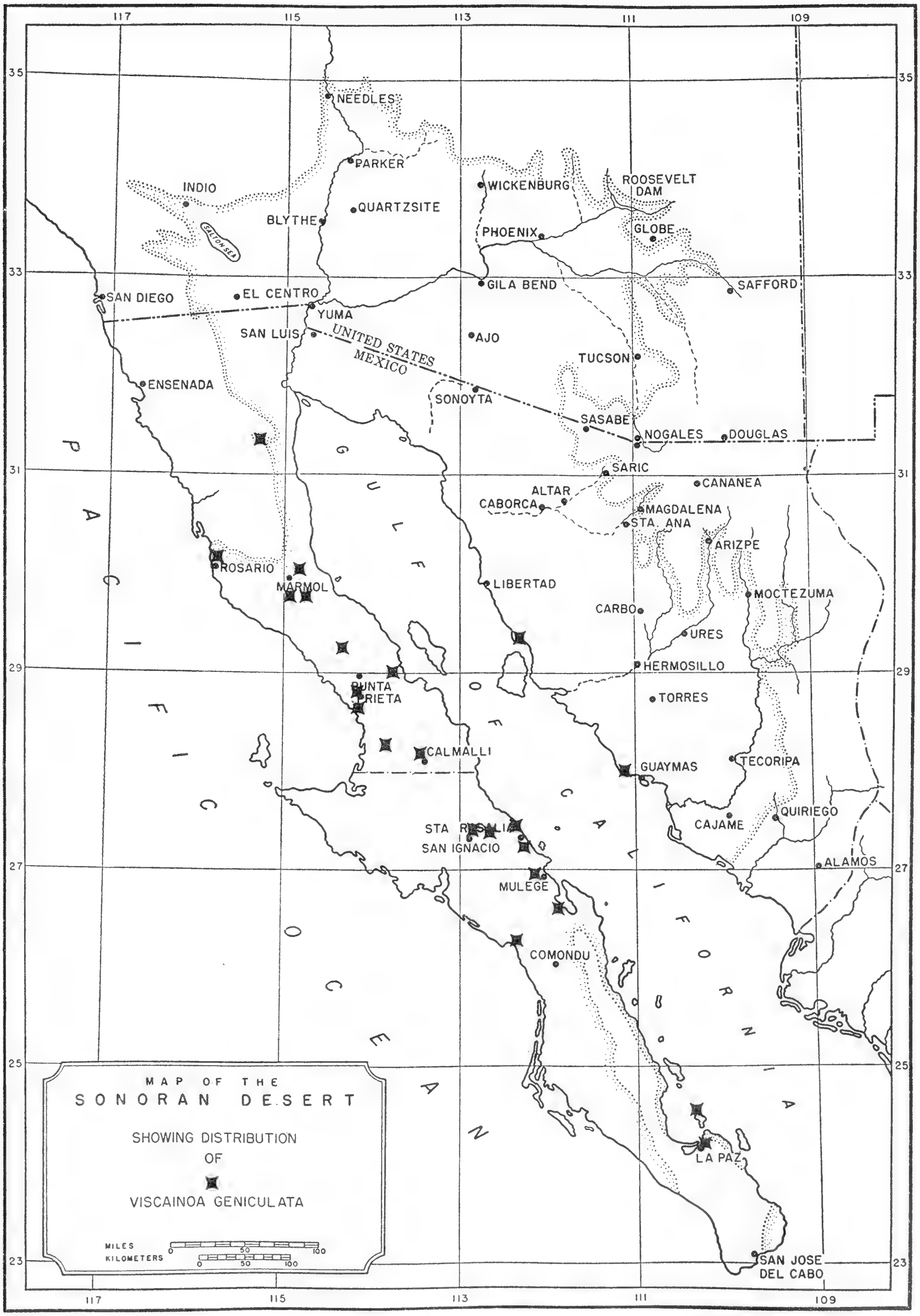
MAP 24. Distribution of *Franseria cordifolia*. Also at Culiacan, Sonora.



MAP 25. Distribution of *Haematoxylon brasiletto*



MAP 26. Distribution of *Simmondsia chinensis*



MAP 27. Distribution of *Viscainoa geniculata*

Literature

Bryan, Kirk. 1925. The Papago country, Arizona. U. S. Geol. Surv. Water Supply Paper No. 499.

Burt, William H. 1938. Faunal relationships and geographic distribution of mammals in Sonora, Mexico. Univ. Mich. Mus. Zool. Misc. Pub. No. 39.

Davis, W. M. 1921. Lower California and its natural resources: a review. Geogr. Rev. **11:** 551–562.

Dice, Lee R. 1939. The Sonoran biotic province. Ecology **20:** 118–129.

——— and Philip M. Blossom. 1937. Studies of mammalian ecology in southwestern North America, with special attention to the colors of desert mammals. Carnegie Inst. Wash. Pub. 485.

Fenneman, N. F. 1928. Physiographic divisions of the United States. Ann. Assoc. Amer. Geographers **18:** 261–353, map.

Goldman, E. A. 1916. Plant records of an expedition to Lower California. Contr. U. S. Nat. Herb. **16:** 309–371.

Harshberger, John W. 1911. Phytogeographic survey of North America. *In* Engler and Drude, Vegetation der Erde, vol. 13, map.

Hilgard, E. W. 1906. Soils. 396 pp. New York.

Humphrey, Robert R. 1933. A detailed study of desert rainfall. Ecology **14:** 31–34.

Ives, Ronald L. 1936. Desert floods in the Sonoyta valley. Amer. Jour. Sci., ser. 5, **32:** 349–360.

McGee, W J 1897. Sheetflood erosion. Bull. Geol. Soc. Amer. **8:** 87–112.

Ochoterena, Isaac. 1937. Esquemas biotípicos y sinecias características de las regiones geográfico-botánicas de Mexico. Ann. d. Inst. Biol. Mexico **8:** 463–597.

Rempel, Peter J. 1936. The crescentic dunes of the Salton Sea and their relation to the vegetation. Ecology **17:** 347–358.

Rübel, E. 1920. Über die Entwicklung der Gesellschaftsmorphologie. Jour. Ecol. **8:** 18–40.

Sanders, E. M. 1921. The natural regions of Mexico. Geogr. Rev. **11:** 212–226.

Shreve, Forrest. 1912. Cold air drainage. Plant World **15:** 110–115.

——— 1915. The vegetation of a desert mountain range as conditioned by climatic factors. Carnegie Inst. Wash. Pub. 217.

——— 1922. Conditions indirectly affecting vertical distribution on desert mountains. Ecology **3:** 269–274.

——— 1934. Rainfall, runoff and soil moisture under desert conditions. Ann. Assoc. Amer. Geographers **24:** 131–156.

——— 1936. The transition from desert to chaparral in Baja California. Madroño **3:** 257–264.

——— and T. D. Mallery. 1933. The relation of caliche to desert plants. Soil Sci. **35:** 99–112.

Spalding, Volney M. 1909. Distribution and movements of desert plants. Carnegie Inst. Wash. Pub. 113.

Sykes, Godfrey. 1926. The delta and estuary of the Colorado River. Geogr. Rev. **16:** 232–255.

——— 1937. The Colorado delta. Carnegie Inst. Wash. Pub. 460.

Tolman, C. F. 1909. Erosion and deposition in the southern Arizona bolson region. Jour. Geol. **17:** 136–163.

Turnage, William V., and A. L. Hinckley. 1938. Freezing weather in relation to plant distribution in the Sonoran Desert. Ecol. Monogr. **8:** 529–550.

PLATES

Close-set mosaic of coarse gravel covering soil near Papago Wells, Pima County, Arizona. The only plants are small individuals of *Plantago*.

PLATE 2

FIG. 1. Bare desert pavement alternating with belts of vegetation in northern Yuma County, Arizona

FIG. 2. Area of fine soil subject to overflow, Yuma County, Arizona

FIG. 1. Hill of sedimentary material capped by basalt, as shown by road cut. Near Gillespie Dam, Maricopa County, Arizona

FIG. 2. Areas of lag talus on hills near Río Sonora below Ures, Sonora

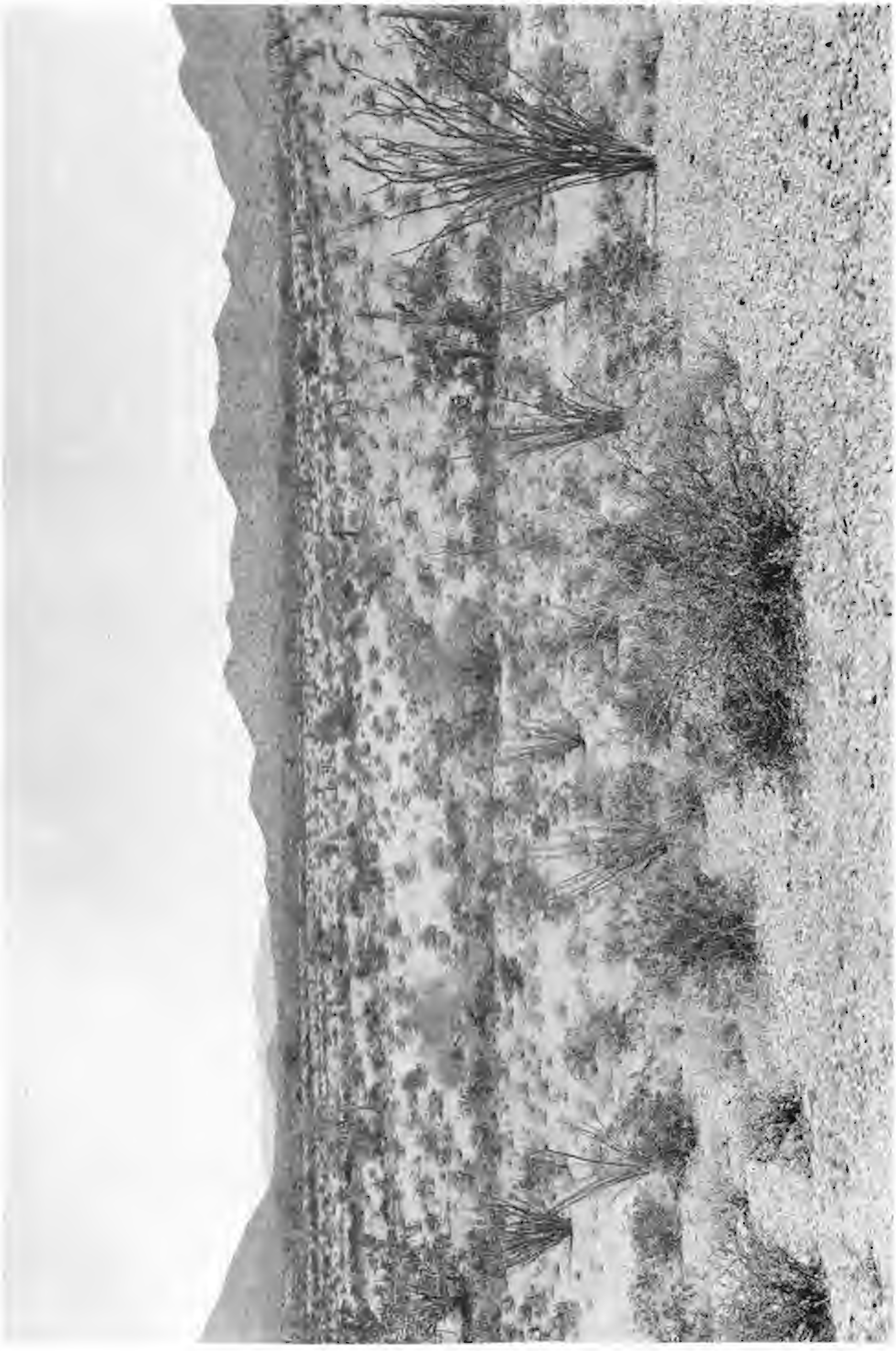
PLATE 4

Granitic hills at base of Cuyamaca Mountains, Imperial County, California

Pure open stand of *Larrea tridentata* on sandy plains south of Pinacate Peak, northwestern Sonora

Looking south toward hills 65 km. west of Sonoyta, Sonora. The sandy soil shows strips almost devoid of plants, and the sand accumulated on the windward side of the hills.

The Salada of the Río Sonoyta, near Quitovaquito, Sonora



Vegetation near Tule Tanks, Yuma County, Arizona. A very open stand of *Franseria dumosa*, *Jatropha cuneata*, *Fouquieria splendens*, and *Carnegiea gigantea*.

South face of the Kofa Mountains, northern Yuma County, Arizona. The steep slopes, active erosion, and hanging talus result in a very light cover of vegetation.

A deeply cut canyon on the north face of the Kofa Mountains. This and similar adjacent canyons are the only Arizona localities for *Washingtonia*.

Coarse outwash plain near Wickenburg, Maricopa County, Arizona, with vegetation characteristic of large areas in the Arizona Upland desert. *Franseria deltoidea, Cercidium microphyllum, Celtis pallida,* and *Acacia constricta.*

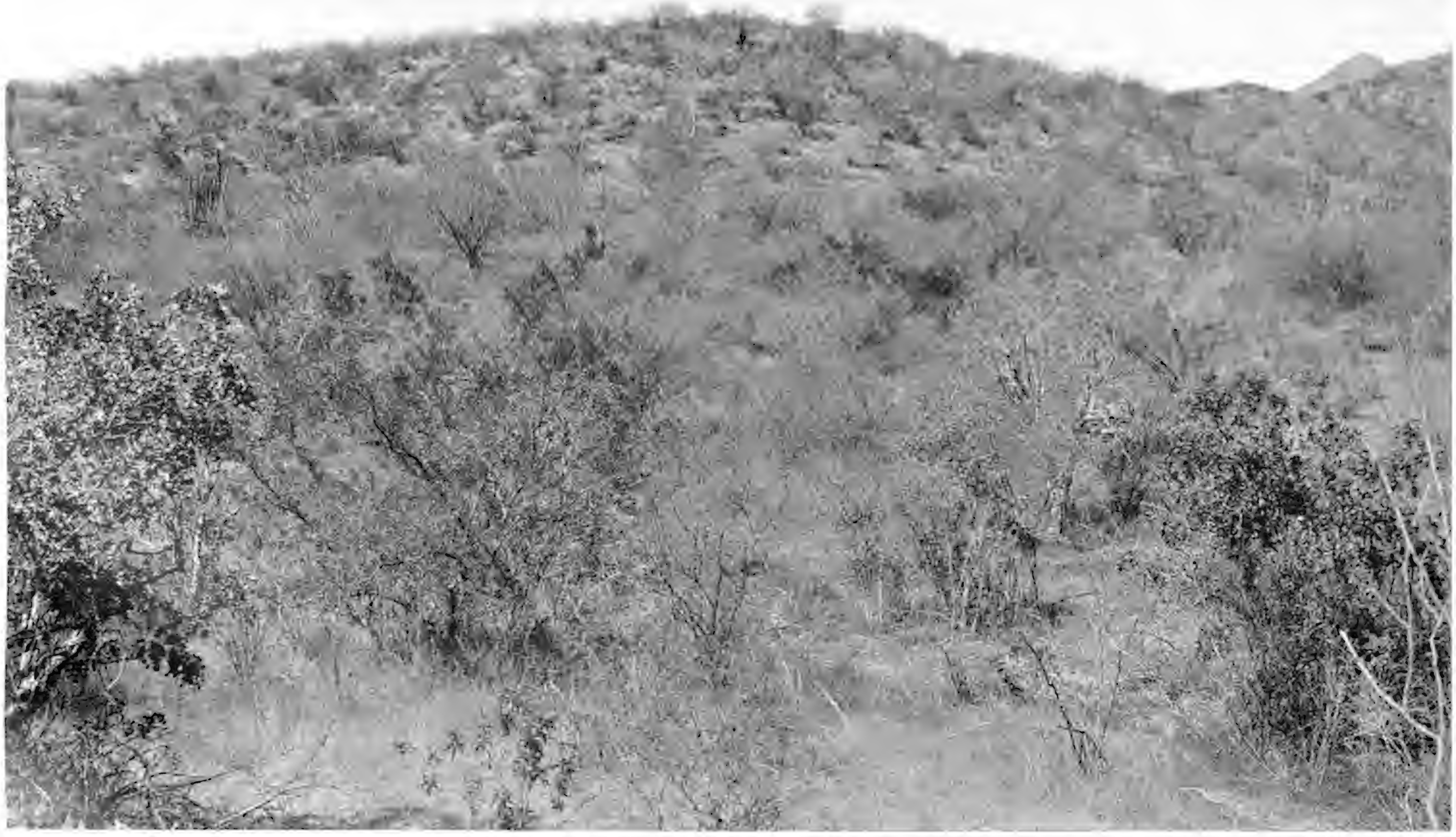
Vegetation near the southern limit of *Yucca brevifolia* in 17 km. north of Aguila, Yavapai County, Arizona, at the southern limit

The upper bajadas near the south end of the Hualpai Mountains, Arizona, are well covered with *Larrea* and *Hilaria mutica,* with infrequent but conspicuous individuals of *Yucca brevifolia, Juniperus utahensis,* and *Yucca schidigera.*

The Plains of Sonora in the vicinity of Carbó are characteristic of a large area in which *Olneya, Cercidium,* and *Encelia* are very abundant and *Larrea* is sharply localized. At right, *Rathbunia alamosensis.*

On the Plains of Sonora 25 km. northwest of Hermosillo. A heavy stand of *Encelia farinosa* with *Prosopis* (leafless), *Guaiacum,* and *Caesalpinia pumila.*

Fouquieria Macdougalii in flower near Carbó, Sonora, with *Cercidium sonorae*, *Rathbunia alamosensis*, and *Lemaireocereus Thurberi*



Low hills 35 km. northeast of Estación Moreno, Sonora. A well mixed stand of *Bursera microphylla, Ipomoea arborescens, Ceiba acuminata,* and *Piscidia mollis*. The only cactus is *Pachycereus pecten-aboriginum*.

In the southernmost arm of the Sonoran Desert 20 km. northeast of Cajeme, Sonora. *Acacia cymbispina, Cercidium sonorae, Jatropha cinerea, Pachycereus pecten-aboriginum, Rathbunia alamosensis, Karwinskia parvifolia* var. *pubescens, Caesalpinia pumila,* and *Opuntia fulgida.*

On the northern edge of the delta of Río Yaqui near Potam, Sonora. With a scattered stand of *Lycium, Atriplex,* and *Stegnosperma* is a rich growth of cacti, including *Lemaireocereus, Lophocereus, Rathbunia, Ferocactus, Opuntia,* and *Mammillaria.*

PLATE 20

Granitic hills 3 km. northeast of Puerto Libertad, Sonora. *Jatropha, Encelia, Fouquieria,* and *Pachycereus.*

Looking north across an arm of the Gulf of California from hills 10 km. south of Puerto Libertad, Sonora. *Idria columnaris* on the slopes.

Volcanic slopes 25 km. north of Laguna Seca Chapala, Baja California. *Prosopis juliflora* var. *Torreyana*, *Atriplex polycarpa*, *Franseria chenopodifolia*, and *Haplopappus sonoriensis*.

A heavy stand of *Idria columnaris* on coarse volcanic soil 20 km. east of Punta Prieta, Baja California. Among the associated plants are *Pachycereus Pringlei, Yucca valida, Machaerocereus gummosus, Pachycormus discolor, Lophocereus Schottii, Agave Shawii, Franseria chenopodifolia, Euphorbia misera,* and *Franseria camphorata.*

Vegetation near the locality shown in plate 23, with characteristic trees of *Pachycormus*

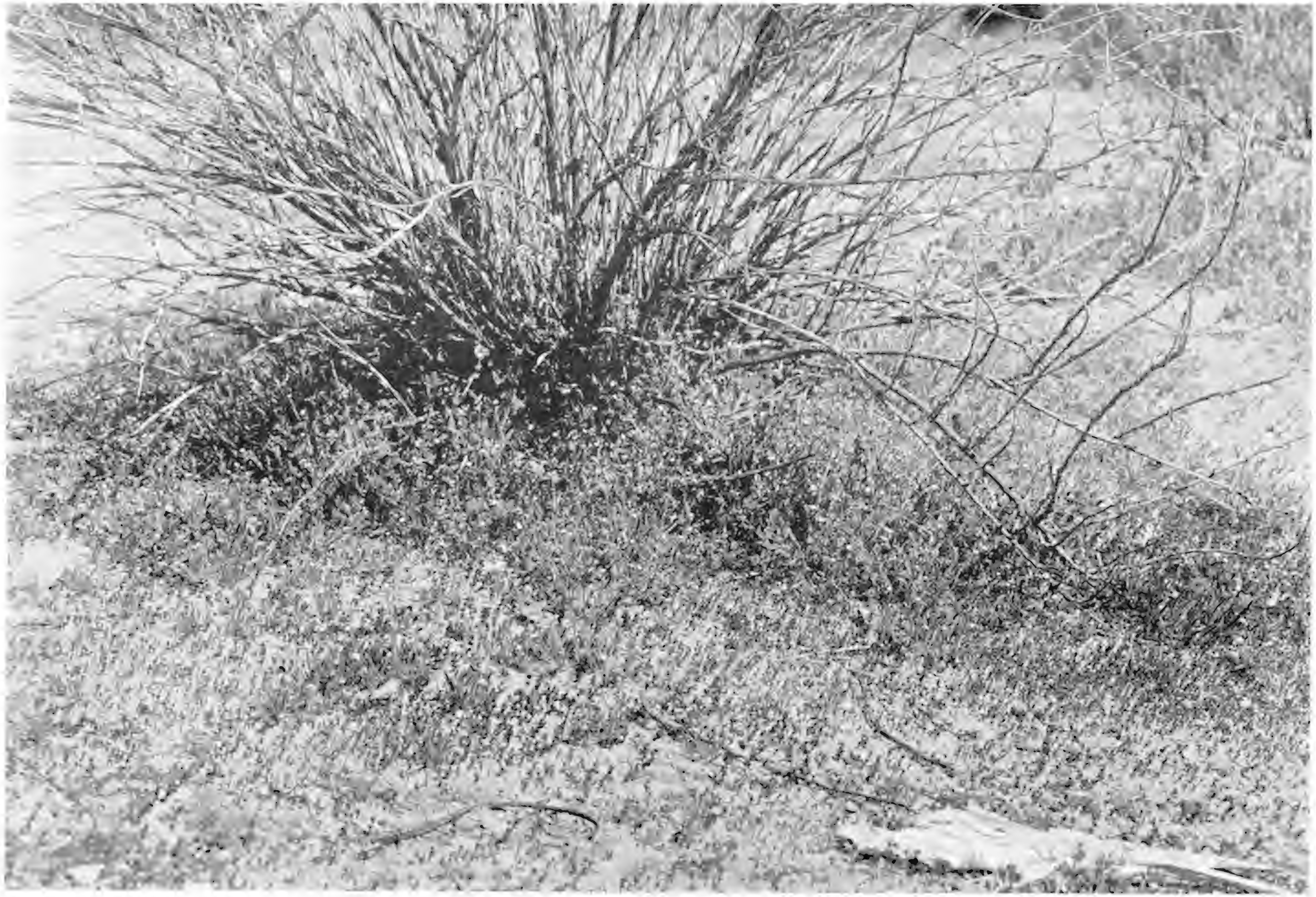
Granite hills and sandy flood plain 25 km. northeast of Pozo Alemán, Baja California. *Yucca valida, Lophocereus Schottii, Opuntia ciribe,* and *Haplopappus sonoriensis.* The sandy surface is well covered with herbaceous ephemerals.

The inner edge of the Vizcaíno Desert 45 km. south of Pozo Alemán, Baja California. The perennial vegetation includes *Yucca valida, Fouquieria peninsularis, Machaerocereus gummosus, Franseria magdalenae, Opuntia cholla, O. calmalliana,* and *Larrea.* The exceptionally heavy growth of herbaceous ephemerals includes *Perityle Emoryi, Cryptantha maritima, Abronia gracilis,* and many other species.

Edge of the lava at the south base of Tres Vírgenes peak, Baja California. *Bursera, Lycium, Encelia, Solanum Hindsianum.*

Slopes of barranca in volcanic mesa 6 km. north of Comondú, Baja California. *Fouquieria peninsularis, Acacia, Lemaireocereus, Pachycereus, Lophocereus.* On the cliffs, *Lysiloma candida* and *Ficus Palmeri.*

Characteristic surface on the Magdalena Plain near El Refugio, Baja California (latitude 24° 50′ N.), showing bare depressions. *Prosopis juliflora* var. *Torreyana*, *Pachycereus*, *Lophocereus*, *Jatropha cinerea*, *Lemaireocereus*, *Machaerocereus*, *Opuntia cholla*, *Fouquieria peninsularis*, and species of *Lycium* and *Suaeda*.



Herbaceous ephemerals around base of *Franseria chenopodifolia* south of San Augustín, Baja California. The tallest plants are *Cryptantha*, the smaller ones *Hosackia*, the smallest *Tillaea*. The outermost dark patches are a blue-green alga.

FIG. 1. Standing skeleton of *Idria columnaris*

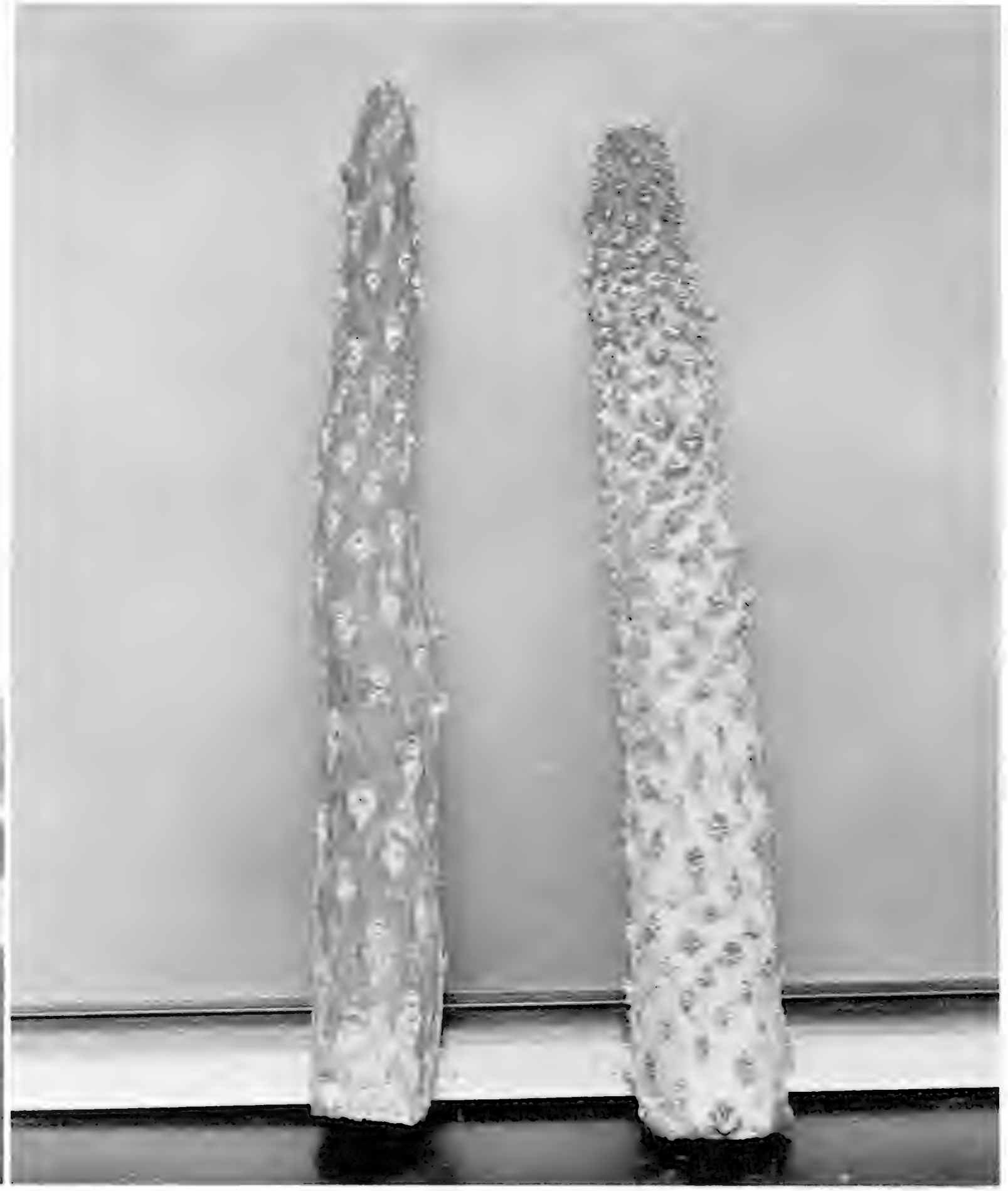


FIG. 2. Growing tips of main stem of *Idria*

FIG. 1. Cross section and surface of trunk of *Idria columnaris*

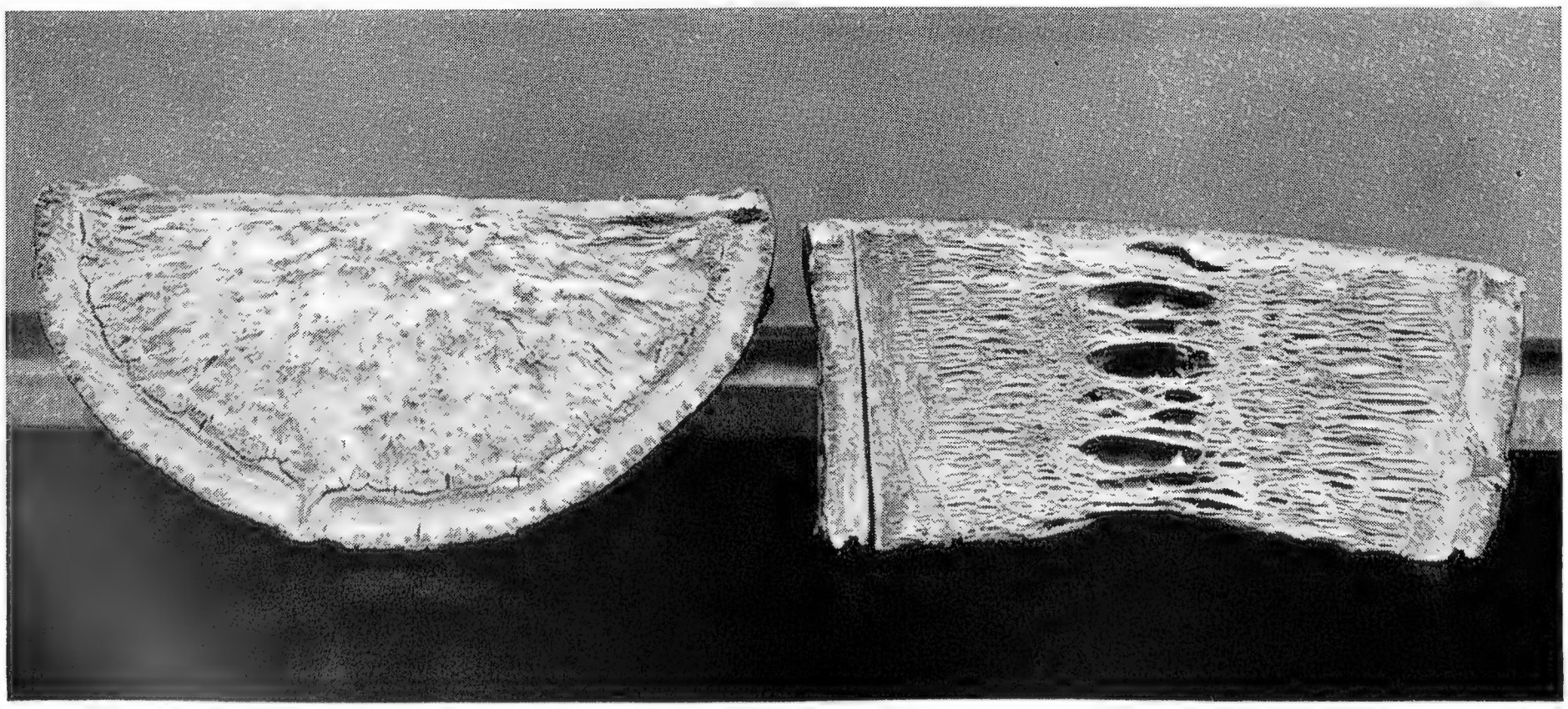


FIG. 2. Cross and vertical sections of trunk of *Idria,* showing large lacunae which accommodate changes in water content of tissue

FIG. 1. Trunk of *Acacia Willardiana*, showing exfoliation of thin layers of white bark

FIG. 2. Mature tree of *Acacia Willardiana*, showing thin crown of cladophylls

Cercidium sonorae in leaf and in flower growing with *Prosopis* on the Plains of Sonora

FIG. 1. Old, many-stemmed tree of *Holacantha Emoryi,* showing dark clusters of persisting fruit. Near Casa Grande, Arizona

FIG. 2. Exceptionally heavy stand of *Pachycormus discolor* on drainage divide of Baja California east of Punta Prieta

Forchammeria Watsoni on outwash plain near La Palma, Sonora

Well developed single individual of *Franseria dumosa* partially in leaf, near Tinajas Altas, Arizona

Index

(Principal references to species are in boldface type)

D

E

F

G

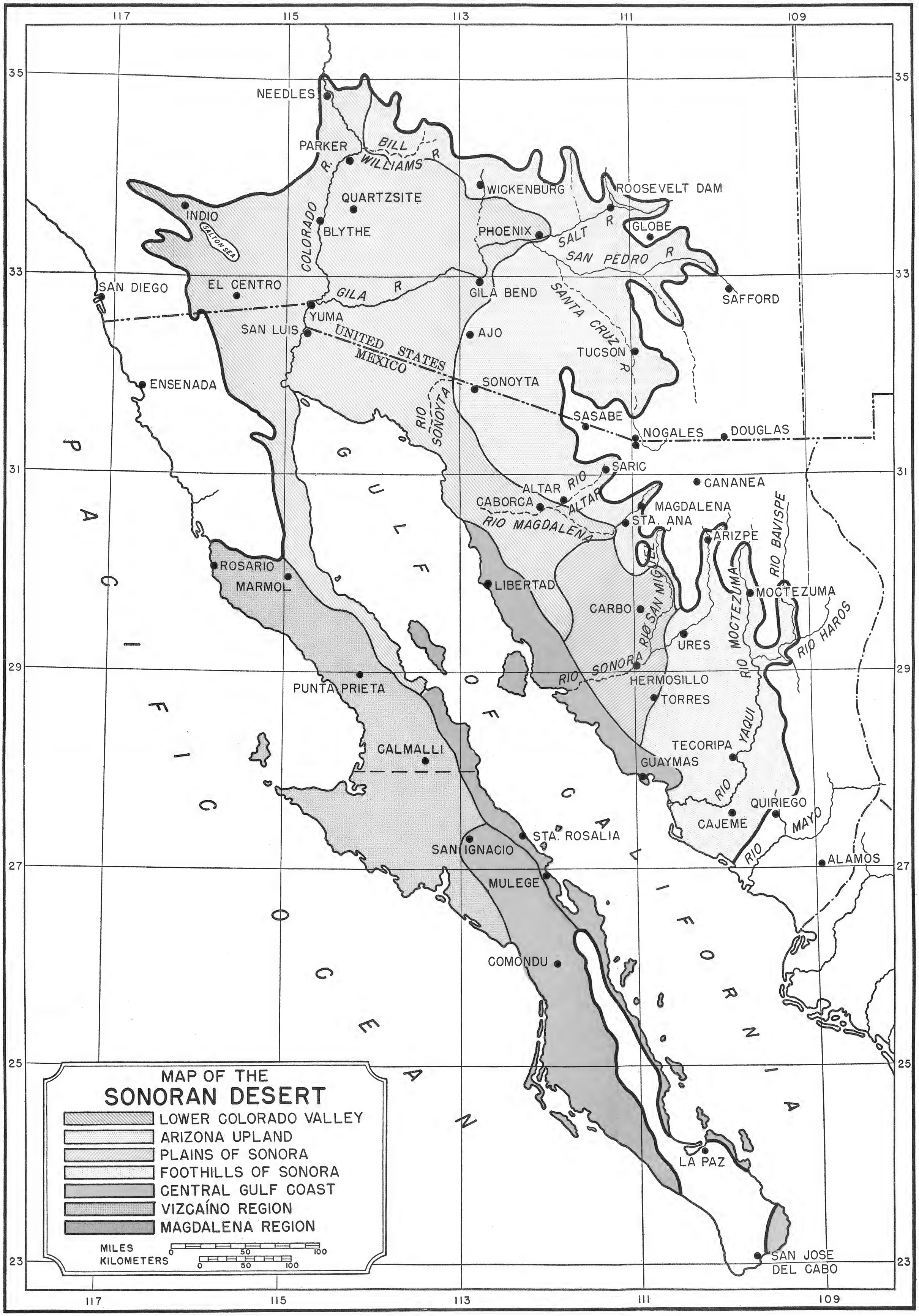
H

I

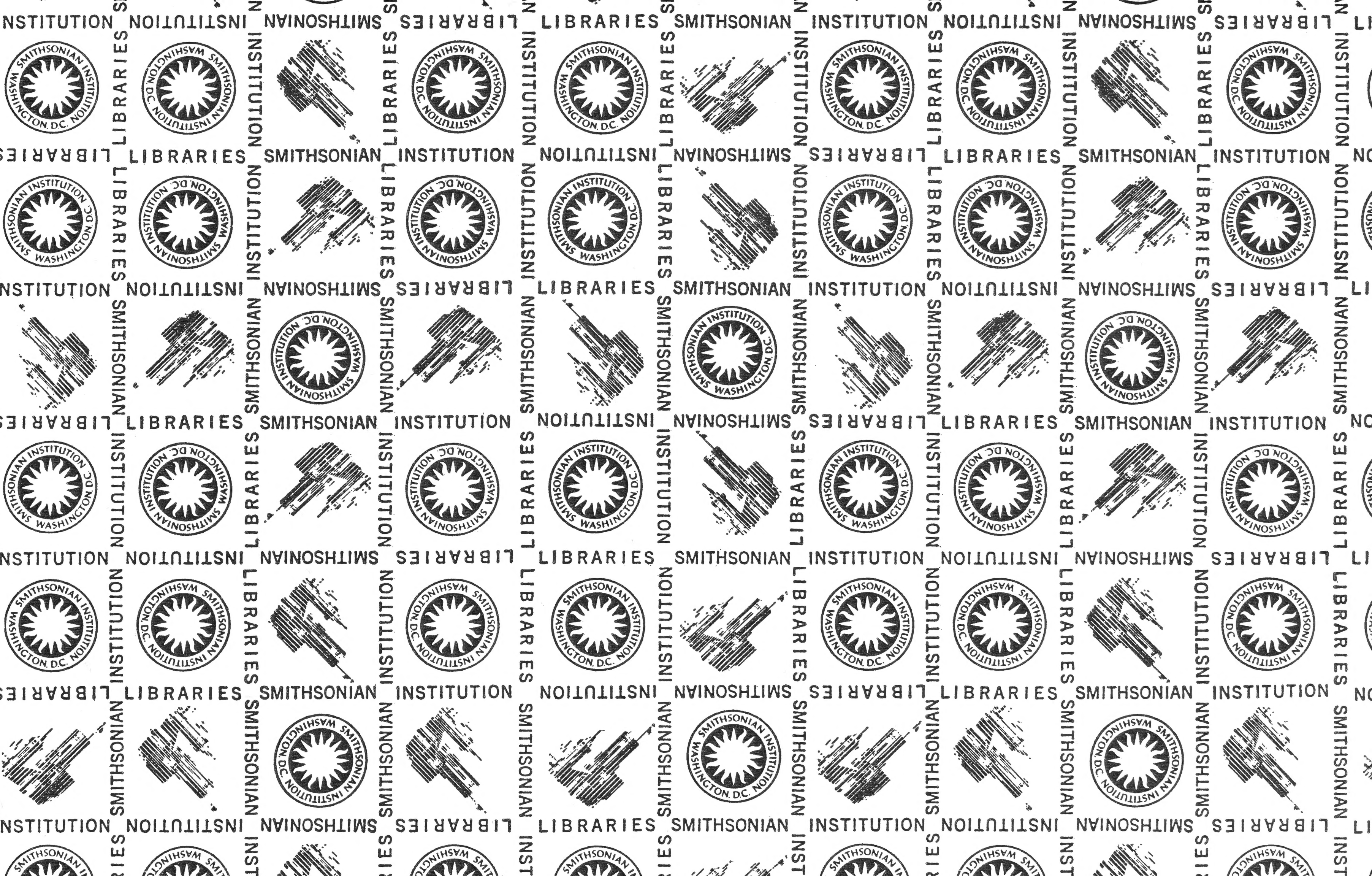
J

N

S



Map 1. The Sonoran Desert and its vegetational subdivisions


SMITHSONIAN INSTITUTION LIBRARIES